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STUDIES ON "SEX-RATIO" IN *DROSOPHILA PSEUDOOBSCURA*. I.[1] SELECTION AND "SEX-RATIO"

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INTRODUCTION

In several species of *Drosophila*, notably in the subgenus *Sophophora*, there exists a genetic condition known as "sex-ratio" which is inherited as though it were due to a sex-linked factor (sr) which causes the progeny of male carriers to consist almost entirely of females. This condition was found by Morgan, Bridges, and Sturtevant (1925) in *Drosophila affinis* and subsequently by Gershenson (1928) in *D. obscura* and by Sturtevant and Dobzhansky (1936) in *D. pseudoobscura, D. persimilis, D. athabasca*, and *D. azteca*.

Unisexual progenies which are the result of sex-linked or sex-limited lethals, or of determined disjunction in XXY females (Gaisinovich, 1928), are accompanied by high egg mortality and are usually half the size of normal progenies. In his analysis of *D. obscura*, Gershenson (1928) found that the size of progenies of sr males equaled and the egg mortality did not exceed that of normal males. He concluded that either sr males produced only X sperm or that the Y sperm was non-functional.

Gershenson also concluded that sr should increase in frequency in a population, unless opposed by natural selection, since an sr male transmits X-chromosomes to all of its offspring while a normal male transmits X-chromosomes to only half of its offspring. The other half of the offspring of normal males, their sons, receive Y-chromosomes.

The purpose of the present studies on *D. pseudoobscura* is to find out whether sr in populations of *D. pseudoobscura* increases in frequency as expected or, if it does not do so, what keeps its frequency in check. It is obvious that elimination of the normal X-chromosomes in a species would result in a population devoid of males. Such a population would face two alternatives—parthenogenesis or extinction.

The action of sr has been analyzed only in *D. pseudoobscura*. Sturtevant and Dobzhansky (1936) found that the Y-chromosome fails to be included in the spindle at the meiotic divisions during spermatogenesis and is lost. The X-chromosome, which shows a four-parted structure at the first metaphase, undergoes two equational divisions during the course of meiosis resulting in the forma-

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tion of four sperm from each primary spermatocyte. Each sperm contains an sr X-chromosome (SR). It follows that a male of this type can produce only female offspring but that these will be as numerous as the combined sexes in normal progenies.

Sturtevant and Dobzhansky (1936) also disclosed the presence of inversions associated with SR. Females heterozygous for normal X-chromosomes (ST) and SR show very little crossing over in the right limb of the X-chromosome, the limb bearing the sr factor. Since the time of that analysis, examination of the salivary chromosomes has shown that the right limbs of SR and ST differ by three inversions, a relatively short terminal, another, quite long, median, and a third, small sub-basal. The first two of these inversions are separated by five sections of the standard map of the X-chromosome (see Plate 4, Dobzhansky and Epling, 1944), the last two by only several bands.

With two exceptions, all flies collected from natural populations have possessed chromosomes identifiable cytologically as either normal (ST) or "sex-ratio" (SR). The two exceptions were males possessing X-chromosomes with terminal but lacking the other two inversions (SR-T). One SR-T was lost, the other retained and tested. It did not have the sr effect. This suggests that the basal inversions contain sr; a suggestion confirmed by the "sex-ratio" behavior of an SR chromosome which lacks the terminal inversion (SR-B). The latter chromosome was obtained in the laboratory by the writer; an analysis of its properties is not yet complete.

The effectiveness of sr is not absolute as we have indicated above; some males do occur in progenies of sr males. Darlington and Dobzhansky (1942) studied the effect of temperature on the frequency of males in these progenies. At 25° C. males comprise 6.2% of the total offspring; at 22° C. (room temperature), 3.7%; and at 16° C., 1.2%. Darlington, because of the general sensitivity of nucleination to temperature, concludes that the nucleic acid charge of the X- and Y-chromosomes is responsible for the abnormal meiosis of sr males. White (1945, p. 197) considers this a possibility which has yet to be proven.

An attempt to localize the action of sr has been made by Holz-Tucker (in mss.). Males were X-rayed in order to obtain aberrations involving SR. Twenty-three SR-autosome translocations were obtained. Each autosome except the dot was involved at least once. The X was broken in a number of places including the borders of the terminal and sub-basal inversions and the middle of the median inversion. Males carrying any of these aberrations produce only female offspring, the characteristic sr effect. Breakage of the X-chromosome, therefore, does not hinder the action of sr.

Material and Methods

Flies for the present studies were collected at Piñon Flats, California in June 1946 by Mr. Alexander Sokoloff. Males were crossed singly to laboratory stocks descended from Piñon females collected earlier; wild females inseminated at the time of collection were placed singly into culture bottles. Of the 144 males tested, 16 gave offspring consisting of 95–100% females. The SR chromosomes carried by these 16 males were the ones used throughout the experiment. No wild females produced unisexual progenies so these cultures were discarded. Evidently these females had been fertilized by several males each or else a number of them would have produced only female offspring.

It is well known that a great variability exists between gene contents of individual chromosomes and that a large proportion of these carry recessive lethal genes (Dobzhansky, Holz, and Spassky, 1942). Although this variation should be more pronounced in autosomes than in sex chromosomes because the latter are car-

ried by males in a hemizygous condition, a gene may not have similar effects in the two sexes. The use of chromosomes obtained from a number of different individuals minimized the probability of obtaining results applicable only to an individual SR chromosome carrying certain genes.

Two constant temperature rooms were used for all experiments; one at 25° C. with a humidity of approximately 70%, the other at 16½° C. with a humidity near 80%. On two occasions the cold room failed to function properly, once for 96 hours and again for 24 hours, and the temperature rose several degrees.

The population experiments were carried out in cages of the type described by Wright and Dobzhansky (1946). Food cups were inserted into the cages three times weekly at 25° and every five days at 16½°. At the time the new cups were added, additional yeast suspension was added to the older cups. Samples of the chromosome populations were obtained by withdrawing egg samples periodically. Each sample consisted of 150 larvae developing from eggs withdrawn over a period of six days. All chromosomal determinations were made cytologically by means of aceto-orcein or aceto-orcein-Karo smears.

Since population cages are maintained for considerable lengths of time, mites present a serious problem. Each of the cages suffered three infections but each time the population (adults and larvae) was saved. The treatment during each infection was the same. Adults were transferred without etherization to a new cage. (Adults of one cage were etherized and examined for mites and mite eggs; neither was found on any of the 2100 flies examined.) Cups were removed from the infected cage and dipped to the rim in a 5% alcoholic solution of benzyl benzoate. If no mites were present on the surface of the food in any cup, that cup was placed in its proper position in the new cage. If mites were found on the food and that cup contained larvae, yeast suspension was added to the food and the churning larvae quickly submerged both mites and their eggs. However, if mites were found in a cup with pupae, that cup was discarded. With this technique all but three or four cups from each infected cage were saved during each infection. Many of the pupae in the discarded cups were empty cases; the fraction of the population lost was negligible.

The Geographical Distribution of SR

The SR arrangement occurs in natural populations over a great portion of the total distribution range of *D. pseudoobscura* (fig. 1). Its highest frequency is reached at the Arizona-New Mexico-Mexico border where it is close to 33% of all X-chromosomes. From this region in any direction there exist downward gradients in the frequency of SR. In the northwesterly direction the frequencies drop from 33% to 17% in central and northern Arizona to 6.3% in the Death Valley region, and finally to 0% in Oregon. The frequency changes in other directions are not quite so uniform but this is in part the result of a less thorough collecting in those directions.

Data have been obtained which permit us to compare the frequency of SR in different years at one locality and even at different seasons of the same year. Collections taken in the Santa Lucia Mountains in California during 1935 and 1940 contained 2% and 5% SR respectively. At Wildrose, near Death Valley, collections taken in 1937 contained 8.1% SR and those of 1940, 11.3%. Neither of these changes is significant.

Samples of *D. pseudoobscura* taken at Aldrich, Texas demonstrate short-term fluctuations in the frequency of SR. The frequencies observed in samples taken in 1939 were: March, 14% (number of chromosomes examined = n = 57); April, 12.5% (n = 425); May, 10.7% (n = 121); and autumn months, 11.5% (n = 26). During 1940, the March, April, and May samples gave the following frequencies: 7.5% (n = 305); 14.8%

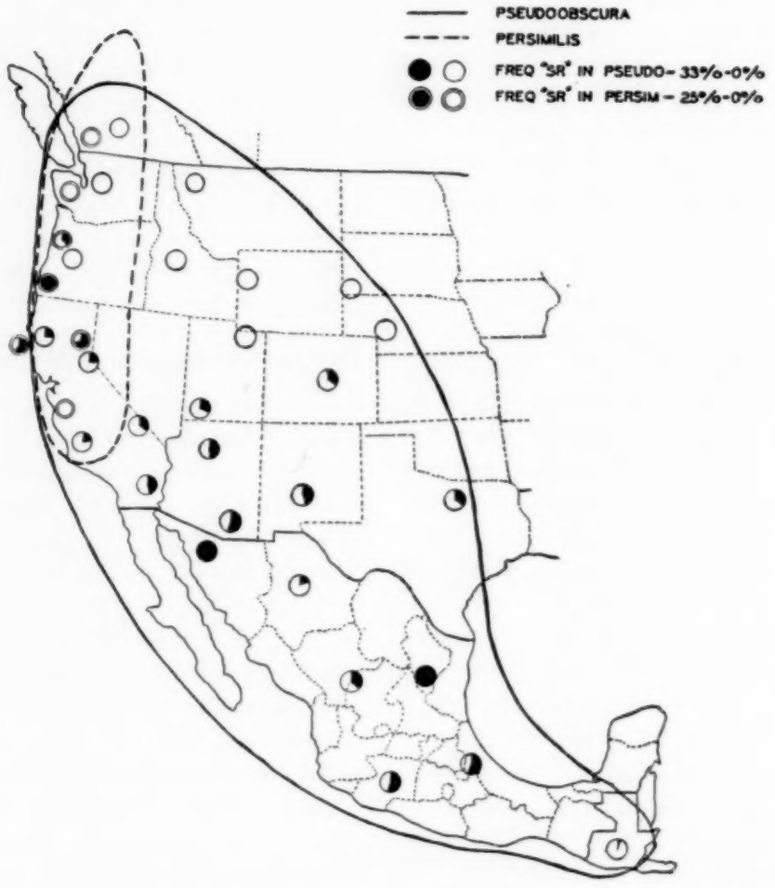

FIG. 1. Geographical distribution of "sex-ratio" in *Drosophila pseudoobscura* and *D. persimilis.*

(n = 169); and 9.1% (n = 22). The probability that the fluctuations observed during either year were chance fluctuations is less than .05. (A detailed analysis of seasonal changes occurring at Piñon Flats and Andreas Cañon, California has been presented previously by Dobzhansky (1943).)

The seasonal fluctuations indicate that the frequency of SR is not independent of the environment. The distribution pattern of SR, then, could be explained in terms of gradients of equilibria ranging from 33% in a region possessing an environment favorable for SR to various smaller values as climatic factors of more distant localities become increasingly adverse to SR.

The inherent tendency of SR to increase in frequency and to spread in a population can be the basis for an alternate hypothesis accounting for the observed distribution. It can be postulated that SR is spreading from a point of origin near the Mexican border, a spread so gradual that the change in frequency from year to year in any one locality cannot be detected.

The data available do not permit a final decision regarding the two hypotheses. Seasonal fluctuations in the frequency of SR, however, show that certain environmental conditions can at times decrease the frequency of SR. Moreover, the theoretical increase of SR expected as a result of its duplication in sr males is quite rapid. We can conclude, therefore, that the actual distribution reflects a modification of the theoretical increase, probably the result of natural selection. This is the thesis to be developed in the subsequent sections. (Data for the above dis-

TABLE 1. *"Sex ratio" in* Drosophila pseudoobscura. SR, percentages of chromosomes which carry "sex ratio"; n, number of chromosomes examined; E, early; M, middle; L, late.

Locality	SR	n
California		
Aspen Valley		
E July 1946	6.7	90
M June 1947	6.9	87
L July 1947	5.3	94
Benson Lake		
L Aug. 1947	0	4
Frazier Mt.		
1947	12.8	141
Lost Claim		
L June 1946	4.0	100
M Aug. 1946	13.0	23
M May 1947	7.1	98
L June 1947	12.8	94
E Aug. 1947	6.1	132
Jacksonville		
L Apr. E June 1946	9.5	126
L July 1946	9.0	89
M May 1947	11.1	190
L June 1947	11.8	152
L July 1947	11.0	146
Mather		
July 1945	4.8	166
L Aug. 1945	4.1	73
L June 1946	10.2	206
M Aug. 1946	7.1	98
M May 1947	7.0	43
L June, E July 1947	6.0	149
L July 1947	9.2	152
Mount Lyell		
L July 1947	0	3
Pate Valley		
L Aug. 1947	0	2
Porcupine Flats		
M July 1947	9.5	21
Timberline		
L July 1946	0	1
Tuolumne Meadows		
L July 1946	0	5
M July 1947	2.7	37
M Aug. 1947	0	9
Keen Camp		
April 1945	17.2	151
April 1946	19.0	226
L June 1946	20.9	267
Piñon Flats		
April 1945	15.1	251
June 1946	23.9	292
Mexico		
Chihuahua		
1947	13.3	211
Durango		
1947	12.1	58
Zachatecas		
1947	0	7

cussion and for figure 1 were adapted from Dobzhansky and Epling, 1944, Part II and from additional data given in tables 1 and 2 which were furnished by Professor Dobzhansky.)

POPULATION STUDIES

To determine what changes, if any, the relative frequencies of SR and ST undergo in freely breeding populations, four population cages were started; in two of these the initial frequency of SR was higher than in the other two; one of each was kept at 25° C. and the other at 16½° C.

Flies for the initial populations were obtained as shown in figure 2. Unknown males from Piñon Flats, California were crossed singly to virgin females from several stocks (ST/ST) descended from females previously captured at Piñon Flats. When larvae appeared, the adults were transferred to fresh culture bottles which were kept at 16½° while the original cultures were kept at 25°. Flies in the cultures kept at 25° emerged while flies in the fresher cultures, kept at the lower temperature, were still larvae. It was possible to determine which of the original males were SR and which were ST

TABLE 2. *"Sex ratio" in* Drosophila persimilis. SR, percentages of chromosomes which carry "sex ratio"; n, number of chromosomes examined; E, early; M, middle; L, late.

Locality	SR	n	Locality	SR	n
California			Mather—*Continued*		
Aspen Valley			L June 1946	22.4	67
E July 1946	15.6	64	M Aug. 1946	20.0	10
L June 1947	24.6	49	M May 1947	17.1	35
L July 1947	20.7	29	L June, E July 1947	15.5	71
			L July 1947	7.1	14
Benson Lake					
L Aug. 1947	13.9	72	Mount Lyell		
			L July 1947	2.6	38
Frazier Mt.					
1947	25.0	4	Pate Valley		
			L Aug. 1947	13.1	38
Lost Claim					
L June 1946	20.0	15	Porcupine Flats		
M Aug. 1946	0	4	M July 1946	33.3	6
M May 1947	12.8	39	M July 1947	11.9	67
L June 1947	16.7	12			
E Aug. 1947	0	2	Timberline		
			L July 1946	8.3	12
Jacksonville			E Aug. 1947	5.9	34
M May 1947	20.0	5			
			Tuolumne Meadows		
Mather			L July 1946	8.3	36
July 1945	17.5	97	M July 1947	14.3	126
L Aug. 1945	20.0	55	M Aug. 1947	6.0	50

by merely observing the number of males in each culture. Males from the normal 25° cultures (ST males) were mated with females from the unisexual 25° cultures (SR/ST females) and these new cultures were also kept at 25°. Since the females from the unisexual cultures were SR/ST heterozygotes, their male offspring were of two types, SR males and ST males. At the time these males were hatching, SR/ST females were hatching in the unisexual, duplicate cultures kept at 16½°. Ten cultures of each of the 16 SR chromosomes were made using single males from 25° and several SR/ST females from 16½°. Approximately half of each of these ten cultures contained SR males; consequently they gave rise only to females (1 SR/SR: 1 SR/ST). The other half of the cultures contained ST males and consequently the flies which came from those cultures were of four types: ST and SR males and SR/ST and ST/ST females.

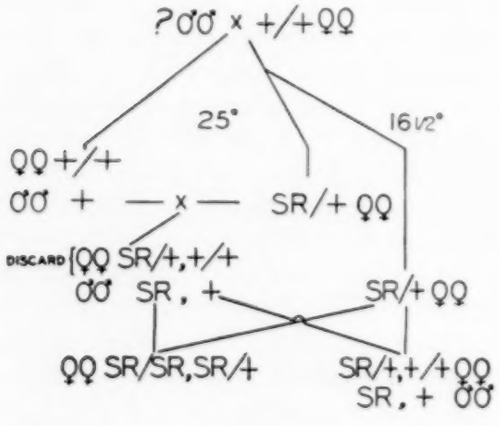

FIG. 2. Series of matings used to obtain flies for experimental populations. (For explanation see text.)

Males for the four cages were collected from the normal cultures and therefore the frequency of SR among males of all cages was 50%. Since females for two cages (Nos. 10 and 12) were collected from the normal cultures, the frequency of SR in the initial female flies of these populations was 25% (1 SR:3 ST).

TABLE 3. *Number of larvae of each genotype and percentage frequency of ST in samples from cages 10 and 11.* Temperature, 25° C.

	Males		Females			Frequency ST (%)	
	SR	ST	SR/SR	SR/ST	ST/ST	Males	Females
Cage 10							
Aug. 15, start	500	500	—	500	500	50.0	75.0
Sept. 20–26	7	24	15	37	74	77.4	73.4
Oct. 11–19	4	40	8	23	75	90.9	81.6
Nov. 16–22	2	48	2	29	84	96.0	85.7
Jan. 1–7	2	57	1	7	83	96.6	95.1
Feb. 6–12	2	53	—	3	92	96.4	98.4
Mar. 13–18	—	64	—	—	86	100.0	100.0
Cage 11							
Aug. 15, start	500	500	500	500	—	50.0	25.0
Sept. 20–26	6	16	22	58	41	72.7	57.9
Oct. 11–19	4	20	11	55	62	83.3	69.9
Nov. 16–22	1	43	7	26	73	97.7	81.1
Jan. 1–7	4	64	—	7	75	94.1	95.7
Feb. 6–12	—	70	—	2	78	100.0	98.8
Mar. 13–18	—	67	—	—	83	100.0	100.0

Females for the other cages (Nos. 11 and 13) were taken from the unisexual cultures; hence, the initial frequency of SR among females in those cages was 75% (3 SR:1 ST).

The four population cages were started August 15, 1946 with 1000 males and 1000 females in each. Cages 10 and 11 were placed in the 25° room; cages 12 and 13, in the 16½° room.

During the time cages 10 and 11 were maintained, six samples of eggs were taken from each. The dates and results of these samples are given in table 3 and in figure 3. It is obvious that the frequency of ST rose rapidly at the expense

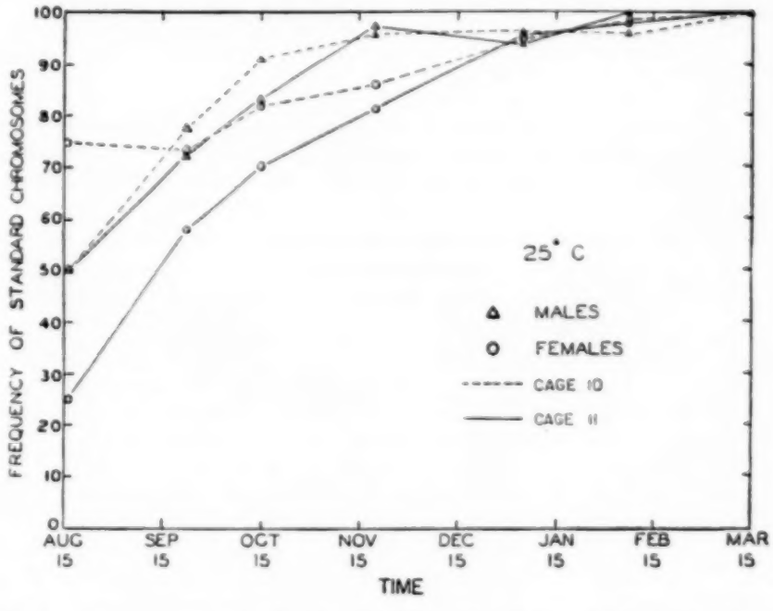

FIG. 3. Changes occurring in the frequency (%) of ST in populations kept at 25° C.

of SR until SR was very nearly, if not entirely, eliminated in both cages after seven months. (The last samples contained no SR in more than 230 chromosomes examined for each cage. The 95% confidence interval (per cent) for the frequency of SR is 0% to 1%.) Not only the overall change but also a majority of changes between successive samples are significant.

To understand more clearly the mode of inheritance of SR and to appreciate the observed increase in frequency of ST, it may be desirable to consider in some detail two generations of a hypothetical population with an initial composition like that of cages 11 and 13. The original genotypic frequencies in those cages were: males, ST—50%, SR—50%; females, SR/ST—50%, SR/SR—50%. The types of matings expected and the zygotic and chromosomal frequencies of the resulting offspring are shown in table 4. The corresponding figures for the second generation have been calculated and are also shown in this table, as well as values observed in the first samples from cages 11 and 13.

One would expect the frequency of ST to be approximately 25% in such populations; instead it is more than twice that value.

The results of samples taken from cages 12 and 13 are given in table 5 and figure 4. The changes observed in these cages resemble in sign those which occurred in cages 10 and 11; ST increases in frequency while SR decreases. However, the rate of increase is not as rapid as in the latter cages and an equilibrium of ST and SR, rather than elimination of SR, is the final result.

A comparison of figures 3 and 4 is difficult because each shows the relationship between chromosomal frequencies and time rather than between frequencies and generations. In the population cages kept at 25° a generation of *D. pseudoobscura* takes approximately 25 days; at 16½°, approximately 40 or 45 days. In figure 5 the data for cages 11 and 13 are replotted by generation. The rate of change is indeed slower in cage No. 13 than in No. 11. Nevertheless, there can be no doubt concerning the increase in frequency of ST and the decrease in frequency of SR in either.

Several conclusions can be drawn from the data obtained by sampling experimental populations. In each of the two constant temperature rooms two populations differing initially in the relative frequencies of ST and SR become very similar in composition. The regularity of

TABLE 4. *Types of matings and the resultant zygotic and chromosomal frequencies expected in cages Nos. 11 and 13.* Original zygotic frequencies: males, ST—50%, SR—50%; females, SR/SR—50%, SR/ST—50%. Matings for the second generation are not shown. The September samples are shown for comparison.

Mating		Zygotic frequencies (%)					Chromosomal frequencies (% ST)	
		Male		Female				
Male	Female	SR	ST	SR/SR	SR/ST	ST/ST	Male	Female
SR	SR/SR	—	—	25.00	—	—		
SR	SR/ST	—	—	12.50	12.50	—		
ST	SR/SR	12.50	—	—	12.50	—		
ST	SR/ST	6.25	6.25	—	6.25	6.25		
Total 1st Gen.		18.75	6.25	37.50	31.25	6.25	25.00	29.17
Total 2nd Gen.		8.85	3.65	53.12	30.73	3.65	29.20	21.73
1st sample, cage 11		4.2	11.2	15.4	40.6	28.6	72.7	57.9
1st sample, cage 13		8.7	15.3	17.3	29.3	29.3	63.9	57.9

TABLE 5. *Number of larvae of each genotype and percentage frequency of ST in samples from cages 12 and 13.* Temperature, 16½° C.

	Males		Females			Frequency ST (%)	
	SR	ST	SR/SR	SR/ST	ST/ST	Males	Females
Cage 12							
Aug. 15, start	500	500	—	500	500	50.0	75.0
Aug. 23–29–Sept. 10–15	8	29	14	45	54	78.4	67.7
Oct. 29–Nov. 2	11	34	24	26	55	75.6	64.8
Dec. 3–8	12	31	11	30	66	72.1	75.7
Jan. 22–27*	8	45	6	18	73	84.9	84.5
Mar. 3–8	6	54	5	20	65	90.0	83.3
May 12–17**	4	47	3	22	74	92.2	85.9
June 12–17	6	61	1	23	59	91.0	84.9
Oct. 8–12–Nov. 4–6	6	63	—	10	71	91.3	93.8
Cage 13							
Aug. 15, start	500	500	500	500	—	50.0	25.0
Sept. 10–16–Sept. 20–26	13	23	26	44	44	63.9	57.9
Oct. 29–Nov. 2	14	26	16	42	48	65.0	65.1
Dec. 4–9	9	17	19	44	50	65.4	63.7
Jan. 22–27*	10	40	8	38	54	80.0	73.0
Mar. 3–8	13	46	15	36	40	78.0	63.7
May 12–17**	5	51	3	23	68	91.1	84.6
June 12–17	3	53	1	24	69	94.6	86.2
Oct. 8–12–Nov. 4–6	4	63	—	8	75	94.0	95.2

* Temperature control failed for 96 hours during this sample.
** Temperature control failed for 24 hours during this sample.

the changes observed and the similarity of the end results indicate strongly that the observed changes were not accidental. Furthermore, the chromosomes reacted differently to different temperatures and humidities. Finally, SR not only failed to replace ST under either set of conditions but, at 25°, SR itself was eliminated.

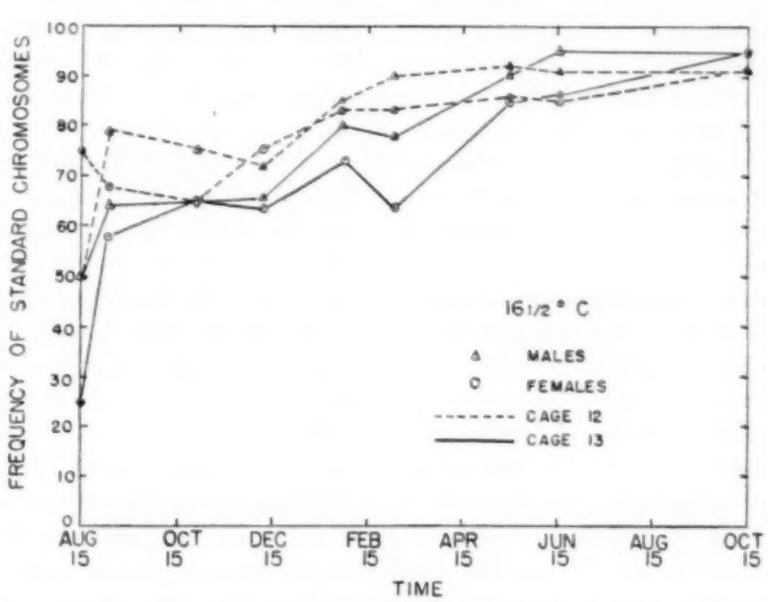

FIG. 4. Changes occurring in the frequency (%) of ST in populations kept at 16½° C.

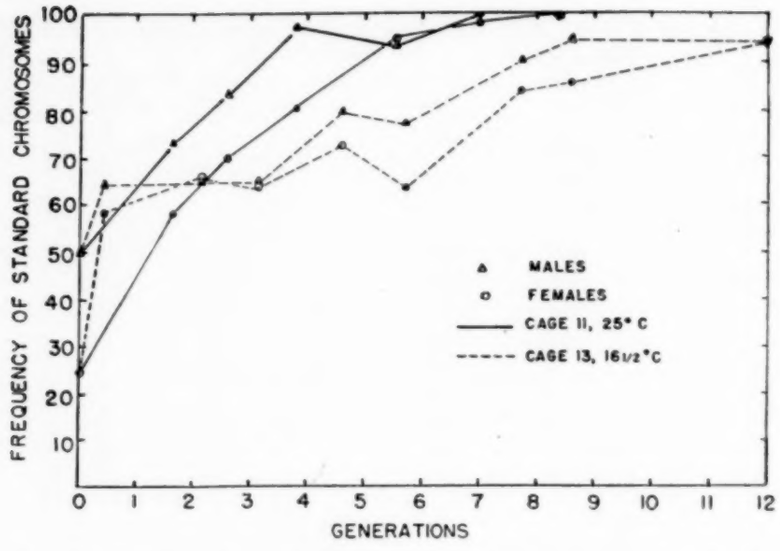

FIG. 5. A comparison of changes occurring per generation in the frequency (%) of ST in populations kept at 25° C. and 16½° C.

At 16½° SR, although not eliminated, became, by far, the rarer of the two arrangements.

ANALYSIS OF SELECTIVE FORCES OPERATING WITHIN EXPERIMENTAL POPULATIONS

Three agencies may alter the frequencies of chromosomal types in populations: mutation pressure, genetic drift, and selection. Of these, only the last two are of importance in the present problem since spontaneous changes in the gene arrangement in chromosomes are exceedingly rare. The effect of genetic drift on the chromosomal frequencies in population cages cannot be ignored but the changes observed in the experimental populations are, in the main, such as can be produced by selection.

The action of selection upon frequencies of chromosomes in a population is subject to experimental investigation. This action must manifest itself through inequalities in the ability of individuals to transmit chromosomes to individuals of the next generation. Inequalities in this ability may be caused by such factors as differential mortality during different periods of life, different degrees of sexual activity, and differences in fecundity and egg viability as determined by the various genotypes. A number of these factors have been chosen for study in an effort to explain the nature of the selective force responsible for the changes observed in the population cages.

1. *Larval competition*

The number of eggs deposited on each cup of food exposed to a population of several thousand flies greatly exceeds the number of larvae a cup of food can support. The actual number of eggs deposited per cup has never been determined but it is estimated to be of the order of ten thousand. Within a week after its initial exposure, the food in each cup is reduced to little more than a liquid matrix within which the larvae constantly churn. Finally pupae form and from these 50–500 flies emerge. The number of adults is only a small fraction of the original number of eggs; at least 90% of the original zygotes perish. If there are differences in survival ability between larvae of different genotypes, a selective mortality would result which would alter the frequencies of the different chromosomal types between eggs and adults.

To determine whether or not the mortality between the egg and the adult stages

is selective, an analysis was made of genotypic frequencies in the eggs deposited on cups and in the adults which finally emerged. The differences found may be loosely described as the result of "larval competition" although the differential elimination need not necessarily be caused by competition nor need it occur during the larval stage since both pupal and early adult stages were included in the time between the two analyses. The technique, in brief, consisted of starting two population cages (one at 25° C., the other at 16½° C.) with large numbers of flies. The zygotic frequencies of the original flies were such that the eggs they laid contained high frequencies of SR males and SR/SR females, i.e., classes suspected of representing the least viable genotypes. The distribution of chromosomal types in the eggs was analyzed by growing larvae hatched from small samples of eggs under optimal conditions and examining the salivary chromosomes of these larvae when they reached full development. Adult males were tested for the presence or absence of the "sex-ratio" effect; the genetic structure of adult females was determined by a cytological examination of larvae produced after insemination by ST males.

A high frequency of SR was obtained in the population of this experiment by means of a series of three crosses. From a number of single pair matings of flies from cage No. 12, ten unisexual cultures and ten cultures containing both males and females were obtained. Males from the normal cultures were crossed singly with females from the unisexual cultures and again some normal and some (seven) unisexual cultures were obtained. At least half of the males in each of the normal cultures were SR, the other males were ST; the females of each of the unisexual cultures were either SR/SR or SR/ST. One hundred cultures were started each with four males from the normal and four females from the unisexual cultures; from these final crosses came the flies which were placed in the cages. It can be seen that exact frequencies of different genotypes among these flies were unknown but that SR was probably the predominant arrangement. This predominance was necessary to compensate for the inviability of SR indicated by the population studies.

The experimental procedure for these cages was a modification of the techniques used with ordinary populations. Into each of the cages were placed 3100 females and 1100–1200 males; one cage was kept at 25° C. and the other at 16½° C. One cup of food was exposed to the flies in each cage for 24 hours whereupon it was withdrawn and a new cup inserted. This process was repeated until 20 cups had been exposed to the flies in each cage. Each cup withdrawn was covered with thousands of eggs as usual. From these eggs two small samples were removed and placed in regular culture bottles; the cup with the remaining eggs was returned to the proper temperature and placed in an empty cage. Since no flies were in the second cage, no eggs were deposited in the cups after the samples were taken. Smears of salivary glands were made of larvae developing from the egg samples; the chromosomal constitution of approximately 35 male and 35 female larvae from each cup was determined. The analysis of these larvae, developed under optimal conditions, provided the information concerning zygotic frequencies of chromosomal types that were present in the egg population.

When pupae began forming in large numbers in the cups which were returned to the cages, the cups were removed and each cup was fastened with Scotch tape to the end of a short piece of 2″ glass tubing. This facilitated the collection of adults.

Males emerging from the cups were crossed singly to virgin females. Normal males, of course, produced offspring of both sexes while sr males produced only females. Observation of flies without etherization was sufficient for scoring cultures containing both sexes; micro-

scopic examination was used to confirm those cultures suspected of being unisexual.

The chromosomal constitution of adult females was determined by cytological examination of their larval offspring. Virgin females were collected from each cup and mated with stock (ST) males. Salivary smears of seven larvae from each female were made and examined. Each female larva contained an ST chromosome from the stock male and another X-chromosome from the mother; the X-chromosome of each male larva also came from the mother. The genotype of the mother was determined when larvae were examined which were of different constitution in respect to their maternal X-chromosomes or when seven larvae were examined all of which possessed the same maternal chromosome. These latter were scored as homozygotes.

The type of determination used for the adult females required a correction factor. Suppose the adult female being tested was actually an SR/ST heterozygote. The first larva examined must carry either the maternal SR or the maternal ST. The probability that the next larva examined will have the same maternal chromosome is ½, that of the third larva, ¼; the fourth, ⅛; and, finally, the seventh, 1/64. This means that 1/64 of the actual SR/ST females were misclassified as either SR/SR or ST/ST; half of those misclassified were included with each type of homozygote. To correct for this error the number of SR/ST females originally scored must be increased by 1/63 (since 63/64 of the true number were scored correctly) and half of this increase must be subtracted from the number scored for each type of homozygote, SR/SR and ST/ST. (The correction factor used was somewhat larger than 1/63 because some determinations were based on fewer than seven larvae.)

The results of the larval competition experiment, given in table 6, demonstrate the effects of selective mortality. At 25° C. SR males survive at a rate less than half that of ST males; SR/SR females only .15 that of ST/SR, the latter being the most viable type of female. ST/ST females are considerably more viable than SR/SR but are inferior to SR/ST. At 16½° differential mortality, though less pronounced, is still considerable. SR males have a smaller survival value than ST males but at 16½° it is .740 as compared with the .407 obtained at 25°. The viability of SR/SR females is more than .60 that of SR/ST females at 16½°. ST/ST females are nearly as viable as SR/ST.

The results obtained from this experiment alone are sufficient to confirm our previous conclusion that selection is the factor responsible for the changes observed in the four original populations.

TABLE 6. *Percentage frequencies of different classes of zygotes in populations before and after larval competition.* Figures have been corrected as explained in text. n indicates the number of individuals tested. The survival values are based upon the relative changes in frequencies.

	Male			Female			
	SR	ST	n	SR/SR	SR/ST	ST/ST	n
25° C.							
Before	55.62	44.38	534	27.41	51.55	21.03	580
After	33.80	66.20	284	5.63	70.06	24.31	273
Survival value	.407	1		.152	1	.847	
16½° C.							
Before	57.12	42.88	562	27.26	45.15	27.59	598
After	49.63	50.37	546	19.27	51.29	29.45	343
Survival value	.740	1		.622	1	.940	

Selection does act within cages and its action does depend upon the environmental conditions.

2. *Longevity of adults*

Adult flies meeting two requirements were used for the remaining analyses. They were "cage" flies, i.e., flies raised in cages, hence, raised under crowded larval conditions, and they were of known genotypes.

Cage No. 12 was the original source of SR for these flies. Single pair matings were made of flies from this cage and, as in the previous experiment, some normal and some (eight) unisexual cultures resulted. Males from the normal cultures were crossed with females from the unisexual cultures and again both normal and unisexual (eight) cultures were obtained. These males were half SR and half ST; females in the unisexual cultures were SR/SR and SR/ST. Twenty-five single pair matings of these males and females were made. Cultures containing an SR male and an SR/SR female or an ST male and an SR/SR female were identified by cytological examination of 9–12 larvae from each culture; these cultures were retained and the others were discarded. Simultaneously with these last crosses, six strains of Piñon Flats flies from among those cultures originally used in the population experiments (ST) were intercrossed to furnish ST chromosomes.

Six population cages were needed to furnish the flies required for the longevity and other experiments. One hundred bottles were needed to furnish the adults for these cages: 40 ST males x ST/ST females, which produced ST males and ST/ST females; 20 ST males x SR/SR females, which produced SR males and SR/ST females; and 40 SR males x SR/SR females, which produced only SR/SR females. Two duplicate sets of cages (one for the warm and the other for the cold room) were started with approximately 500 flies of each sex in each cage. Each set consisted of three cages containing parent flies of the same types as the three groups of bottles described above. The flies developing in each of these cages were, consequently, of known genotypes; in one cage there were ST males and ST/ST females, in the second SR males and SR/ST females, and in the third only SR/SR females. Fresh cups of food were inserted into these cages on every second day. When pupae began forming in any cup in large numbers, this cup was withdrawn and fastened to a short piece of 2″ glass tubing to facilitate the collection of adults. From 16 to 20 cups were exposed to the flies in each cage before the parental flies were discarded.

The longevity of flies of each genotype was determined for both the warm and the cold rooms. Flies were collected daily and were placed into ½ pint culture bottles. A set of five bottles each containing 90–100 flies collected within a period of 48 hours was used to represent each genotype (SR males, at 25°, were represented by 4 bottles). At weekly intervals the survivors of each bottle were transferred to a fresh bottle and the number of deaths occurring during the week was determined by counting the dead flies.

The longevities of the two types of males are slightly but significantly different at 25° C. Of the three types of females, the longevity of ST/ST is nearly identical with that of SR/ST; that of

TABLE 7. *Mean longevities and relative longevities of flies in bottles with food*

	Genotype	Mean longevity (days)	Relative longevity
25° C.	♂♂ SR	39.409±.846	1.086
	♂♂ ST	36.275±.846	1
	♀♀ SR/SR	30.797±.595	.645
	♀♀ SR/ST	47.717±.945	1
	♀♀ ST/ST	45.614±.925	1.000
16½° C.	♂♂ SR	64.808±1.20	1.113
	♂♂ ST	58.215±1.17	1
	♀♀ SR/SR	79.904±1.39	.819
	♀♀ SR/ST	97.526±1.90	1
	♀♀ ST/ST	92.052±2.18	1.000

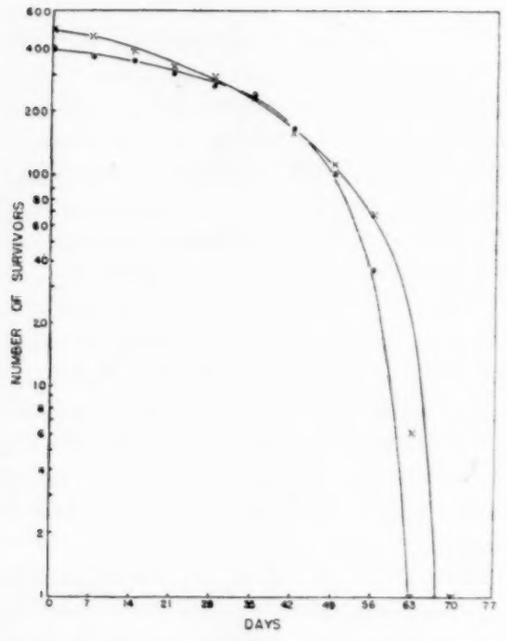

FIG. 6. Survivorship curves for males kept with food at 25° C. SR, ○——○; ST, ×——×.

SR/SR differs markedly from the other two. (See table 7, and figures 6 and 7.) If the mean longevities of ST males and SR/ST females are the standards for the two sexes, SR males have a relative mean longevity of 1.086; ST/ST females, 1.000; and SR/SR females, .645.

At 16½° C. (see table 7 and figures 8 and 9) SR males again have a significantly greater mean longevity than ST males; the realtive mean longevities are 1.113 and 1 respectively. The three types of females have the following relative mean longevities: SR/SR, .819; SR/ST, 1; and ST/ST, 1.000.

An additional study estimating the longevity without food was made with flies at 25° C. Flies were collected every eight hours and were placed into clean 1″ × 3¼″ shell vials, 15 flies of a given genotype per vial. 150 flies (10 vials) of each genotype were studied. The vials were stoppered with thin tufts of cotton and were placed upright within a 14″ pyrex desiccator which contained a concentrated NaCl solution. A band of white cardboard kept the vials in position around the edge of the desiccator and made it possible to count the dead and living flies by inspection through the wall of the desiccator. The number of survivors was recorded every eight hours.

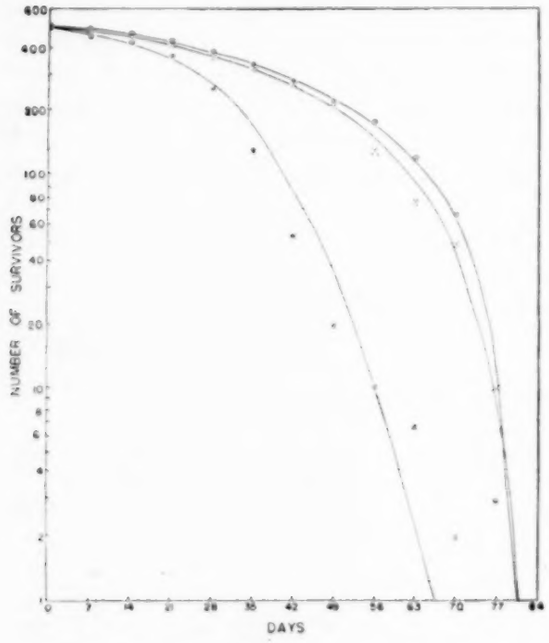

FIG. 7. Survivorship curves for females kept with food at 25° C. SR/SR, □——□; SR/ST, ○——○; ST/ST, ×——×.

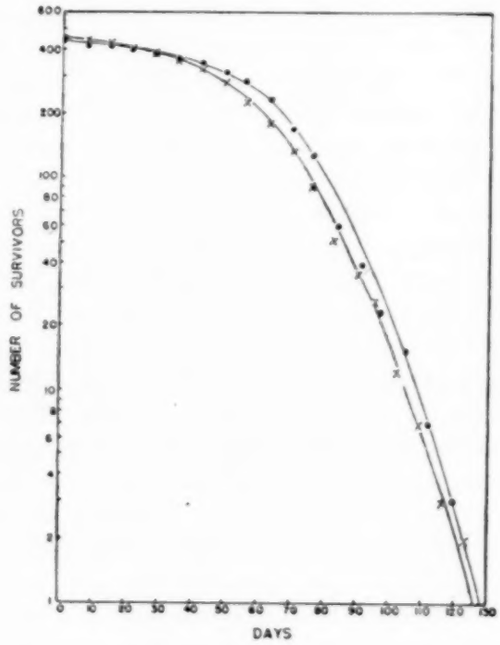

FIG. 8. Survivorship curves for males kept with food at 16½° C. SR, ○——○; ST, ×——×.

Without food, the two types of males have mean longevities which are not significantly different. Each of the three types of females differs significantly from the others: SR/ST lives the longest, ST/ST next, and SR/SR the shortest length of time. (See table 8 and figures 10 and 11.)

The biological meaning of the data on longevity without food is difficult to evaluate. In the experiments with food it could be assumed that the food served both the adults and the larvae developing from eggs deposited on it by the adult females; this assumption may be regarded as justifying the computation of selective values based on relative mean longevities.

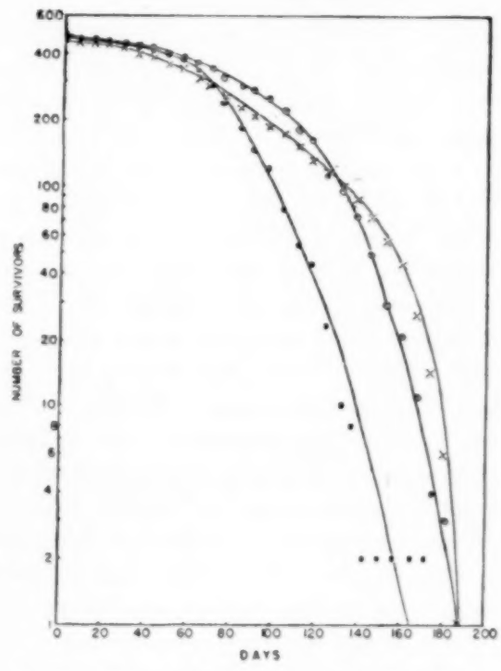

FIG. 9. Survivorship curves for females kept with food at 16½° C. SR/SR, □——□; SR/ST, ○——○; ST/ST, ×——×.

TABLE 8. *Mean longevities of flies kept in vials without food.* Temperature, 25° C.; humidity, 92%

Genotype	Mean longevity (hours)
SR	46.83±.60
ST	47.68±.55
SR/SR	48.05±.69
SR/ST	52.80±.71
ST/ST	50.13±.75

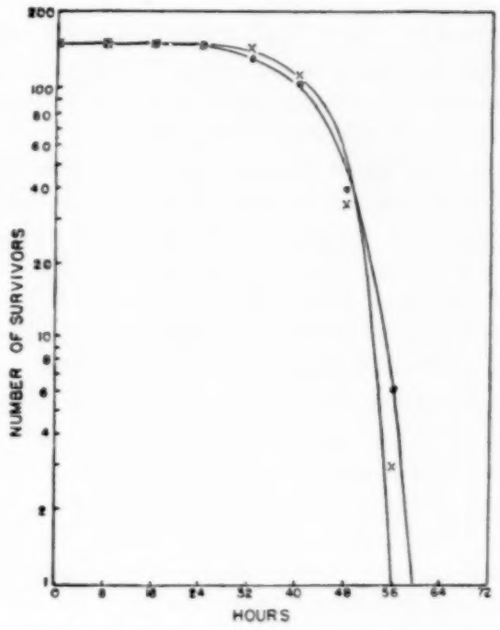

FIG. 10. Survivorship curves for males kept without food at 25° C., humidity, 92%. SR, ○——○; ST, ×——×.

When flies are deprived of food, however, the females have nothing on which to deposit eggs; hence, in the absence of food, relative selective values are deter-

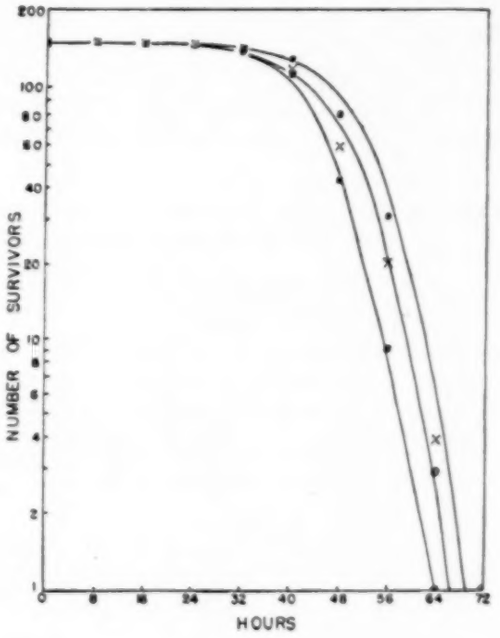

FIG. 11. Survivorship curves for females kept without food at 25° C., humidity, 92%. SR/SR, □——□; SR/ST, ○——○; ST/ST, ×——×.

mined not by mean longevities but by the relative frequencies of survivors at an arbitrarily chosen time. It can be estimated from figure 11 that if newly emerged adult females have no food for 16 hours, the selective values for the three types are equal, while after 48 hours without food the survival value of SR/SR is .544 and that of ST/ST is .735, and after 64 hours these values have dropped to .143 and .572 respectively. The survival values, then, depend upon the length of time the adults must exist without food. (It may be mentioned that similar considerations were applicable in the study of "larval competition"; the data obtained indicate the frequencies of genotypes surviving the larval stage and not the mean longevities of larval genotypes. This is true because a larva which succumbs after five days of competition, for instance, has contributed no more towards the biotic potential of its generation than one which succumbed after one or two days.)

3. *Fecundity*

A female influences the chromosomal frequencies in a continuous population through the eggs she lays; females which lay the greatest number of eggs, other factors being equal, make the largest contribution to the succeeding generations. Selection acting upon the frequencies of SR and ST in a population, then, may do so through differential fecundities of the three types of females.

The fecundity of females of the three genotypes was determined at both 25° C. and 16½° C. by testing 80–90 females of each type. The females were placed in clean 1" × 3¼" shell vials, five females and five ST males in each vial. Periodically throughout their life span the number of surviving females in each vial and the number of eggs these females deposited in 24 hours was determined. Food for the flies was placed on wooden spoons which were inserted into the vials; this food was moistened with yeast suspension daily in the warm room, twice weekly in the cold room. For egg counts the wooden spoons were replaced by composition spoons carefully filled with fresh, yeasted food. After 24 hours exposure, these spoons were withdrawn and replaced by wooden spoons filled with fresh food. The eggs deposited on the composition spoons were counted under a binocular microscope. The females in each vial were also counted at this time. As the females died, vials were consolidated so that the number of females per vial was maintained at approximately five. Fresh males were added to vials when-

TABLE 9. *Fecundity of females of different genotypes at 25° C.* D is the age of females in days; n, number of surviving females; E, total eggs laid in 24 hours; E/n, number of eggs laid per female in 24 hours

D	SR/SR			SR/ST			ST/ST		
	n	E	E/n	n	E	E/n	n	E	E/n
0	85	0	0	90	0	0	85	0	0
2	85	0	0	90	0	0	85	0	0
3	81	260	3.22	90	196	2.18	80	72	.90
6	*67	1023	15.27	*68	1491	21.95	73	653	8.94
9	70	558	7.97	78	1184	15.20	59	656	11.15
13	61	564	9.25	75	1122	15.00	51	761	14.95
20	41	151	3.68	50	346	6.92	17	195	11.42
27	9	39	4.34	22	329	14.96	15	63	4.19
34	3	0	0	7	67	9.58	11	29	2.64
41	0	0	—	0	0	—	0	0	—
Total eggs		2595			4735			2429	

* 2 vials SR/SR and 3 vials SR/ST not tested.

TABLE 10. *Fecundity of females of different genotypes at 16½° C.* D is the age of females in days; n, number of surviving females; E, total eggs laid in 24 hours; E/n, number of eggs laid per female in 24 hours

D	SR/SR			SR/ST			ST/ST		
	n	E	E/n	n	E	E/n	n	E	E/n
0	80	0	0	85	0	0	80	0	0
9	78	36	.461	84	37	.440	70	287	4.100
14	78	380	4.872	84	246	2.929	69	715	10.362
21	76	610	8.026	83	713	8.590	63	750	11.905
28	74	612	8.270	72	1221	16.958	57	561	9.842
35	70	636	9.086	62	1093	17.629	49	697	14.224
42	53	330	6.226	50	603	12.060	39	281	7.205
49	46	135	2.935	44	1123	25.523	37	370	10.000
70	29	193	6.655	34	390	11.741	29	334	11.517
84	21	36	1.714	27	214	7.926	18	156	8.666
98	13	57	4.385	24	185	7.708	17	129	8.182
137	0	0	—	0	0	—	0	0	—
Total eggs		3025			5825			4280	

ever fewer than three males remained. Flies were transferred to clean vials when necessary, usually every week at 25° C., every two weeks at 16½° C.

Table 9 gives the data obtained from the fecundity experiments at 25° C. Females of all genotypes begin laying at the age of three days. SR/ST and SR/SR females reach their peak of productivity on the sixth day and decline after this time; the productivity of SR/SR females declines much more rapidly than that of SR/ST. ST/ST females reach their peak of productivity near the 13th day; the increase and decrease of productivity on either side of this maximum are quite symmetrical.

Data on the fecundity of females kept at 16½° C. are given in table 10. At this temperature egg laying started on the seventh or eighth day and continued for more than 14 weeks. All females at 16½° C. maintained a high productivity during the greater part of the experiment: ST/ST females had nearly reached their peak of productivity by the second week, the others attained theirs only after three or four weeks had elapsed.

The genetic consequences of fecundity differentials do not depend upon egg production (eggs per female) alone; the number of females, a factor governed by longevity, is also involved. If adaptive values for the different genotypes are computed on the basis of the average number of eggs produced per female per 24 hours during her lifetime, these values multiplied by the relative mean longevities give imperfect estimates of adaptive values for, indeed, the rate of egg production is not uniform throughout the life of a female. This non-uniformity, in a population of flies of equal age, raises the following difficulties: No eggs are produced by the group during the first two days when practically all the flies are alive, many eggs are produced by each female when most of the females are still living, and then fewer and fewer eggs are produced per female while there are fewer and fewer survivors to produce them. Since the period of maximum egg production of ST/ST females follows that of SR/SR and SR/ST females by a week at 25° C., it seems desirable to calculate the adaptive values by a method other than the approximation given above.

Two sets of data on longevity are available for use in computations involving rates of egg production and numbers of flies: data given in the preceding subsection and data obtained during the course of the experiment now under consideration. Each set has its advantages and

disadvantages. The data given previously were based on large numbers of flies which underwent a minimum of handling; hence the resulting survivorship curves appear more reliable. These curves apply, however, to virgin females and, because of the conditions used, the longest survival time is approximately twice that obtained for flies used in the fecundity experiments. On the other hand, the flies used in the fecundity experiments were the ones which were producing the eggs and whose longevities are most closely concerned with the present problem. The original numbers of these flies, however, were small; these flies were handled constantly; and accidental deaths were rather numerous.

Table 11 gives adaptive values (25° C.) computed by several methods in order that the effects of the above considerations may be evaluated and compared. The first computation is based upon the average number of eggs produced per female throughout the course of the experiment; this value multiplied by the relative mean longevities is also given. The second estimation involves the longevities of the flies used during the fecundity experiment. This method consists of dividing the total eggs produced by flies of each type during the experiment by the original number of flies of each type; this gives the overall productivity of the flies tested and corrects for the number of survivors at various times and for the rates of oviposition at those times. Computations three and four correlate the fecundity and the regular longevity experiments. Since the duration of the latter experiments was not equal to that of the former, a correction factor was introduced. Computation three involves the use of a constant (approximately 2) obtained by dividing the duration of the longevity experiment (in days) by that of the fecundity experiment. The fourth calculation is based on the assumption that the correction factors should increase with time. The equation $X = Y + Y \log cY$ (where X is time in the longevity experiment, Y is time in the fecundity experiment, and c is a constant chosen to equate the times at which all

TABLE 11. *Relative fecundities at 25° C. computed by different methods (see text).* Both the number of eggs per female (No.) and the adaptive value (A.V.) obtained by each method are given. Those methods which take into account both egg production and the longevity of the females are marked (*)

	Females		
	SR/SR	SR/ST	ST/ST
(1) Eggs/female (average of all counts).			
No.	5.2	8.3	5.1
A.V.	.627	1	.615
*A.V.	.404	1	.615
(2) *Total eggs/original number of females.			
No.	30.53	52.61	28.58
A.V.	.580	1	.543
(3) *Computed from eggs/female and number of survivors at time of egg counts. Correlation of longevities made by multiplication by a constant			
No.	29.80	71.18	41.59
A.V.	.419	1	.584
(4) *As in (3) except that correlation of longevities is made by multiplication by an increasing factor.			
No.	32.17	71.56	45.73
A.V.	.450	1	.639

the flies had died in the above experiments) was chosen for this purpose. This method has the advantage of retaining the start of oviposition at a time consistent with routine observations and with experimentation (Dobzhansky, 1935).

A comparison of the results of the various computations shows that different adaptive values are obtained at 25° C.: values ranging from .404 to .580 for SR/SR females and from .543 to .639 for ST/ST females. Computation No. 2 indicates that SR/SR females have a higher adaptive value than ST/ST females but the other computations indicate the reverse. At 16½° C. the relative fecundities have been determined by the first two methods of computation only (see table 12); the average number of eggs deposited per female throughout the experiment and the total eggs produced by flies of each type divided by the original numbers of flies. As at 25° C., the results of the computations differ slightly; nevertheless, SR/SR females appear to be only half as productive as SR/ST females, whereas ST/ST females are quite similar to the latter. Although the results obtained by different methods of estimation vary somewhat, the conclusion can be drawn that differential fecundities do exist and, hence, that selection is acting at this period of the reproductive cycle.

4. *Sexual activity*

In a population of sexually reproducing individuals, the transmission of chromosomes and genes from one generation to the next depends in part upon the activity the various individuals exhibit in the acquisition of mates. Chromosomes (or genes thereon) which decrease or increase the sexual activity of their bearers correspondingly alter their frequency of transmission. In the case of males the relationship between activity and adaptive value based on activity is direct and simply determined; in the case of females there are factors which interfere greatly in the calculation of adaptive values. As an example of one of these complications it is sufficient to note the retention of eggs by virgin females. A female may require more than a normal amount of courting before she accepts the advances of a male; if she retains her eggs until this time, and is capable of laying as many eggs as other females, her behavior has selective significance only in that it contributes an increment to the total generation time. The determination, then, of adaptive values of sexual activity for females becomes a complex problem involving egg production, time of insemination, and mutual influences of these two factors. The present section, therefore, is an analysis of the sexual activity of males only.

The technique used to study sexual

TABLE 12. *Relative fecundities at 16½° C. estimated by methods 1 and 2 as explained in text.* Both the number of eggs per female (No.) and the adaptive value (A.V.) obtained by each method are given. Those methods which take into account both longevity and egg production are marked (*)

	Females		
	SR/SR	SR/ST	ST/ST
(1) Eggs/female (average of all counts)			
No.	4.89	8.97	8.11
A.V.	.545	1	.903
*A.V.	.446	1	.903
(2) *Total eggs/original number of females			
No.	37.81	68.53	53.50
A.V.	.552	1	.781

activity consisted of determining how many females a certain number of males could inseminate in a given time. The flies used in this experiment came from the cages described on page 201. These flies were collected daily to insure virginity of females. Before testing, all flies were aged in ½ pint bottles (sexes isolated); at 25° C. males were aged from 5 to 14 days, females, from 6 to 20 days; at 16½° C., males, from 10 to 14 days, females, from 10 to 17 days.

The experiment was composed of a number of separate runs; a run consisted of several vials of one type of male confined with two types of females and an equal number of vials of the other type of male confined with the same two types of females. Each vial contained ten males and 20 females, ten of each type. The males in each run were uniform in age; the two types of females were not always of the same age but the choice offered to males of one type was always identical with the choice offered to the other males.

Females were marked by clipping the tip of one wing, the left wing of one type and the right wing of the other. After the clipping, ten females of each type were placed in vials with food and kept in the proper constant temperature room. Males, also, were placed in vials with food and returned to the proper temperature. All flies were left overnight to recover from the etherization.

The actual experiment began by transferring the females and the males into clean 1″ × 3¼″ shell vials (cooled overnight at 16½° C. for experiments at that temperature) and leaving them together for two hours. At the end of that time the flies were etherized, counted, males were destroyed, and the females were placed in vials with food to await dissection. Occasionally flies were lost between the original count and the test; if no more than one male, one female, or one female of each type were lost, the results were included in the data. The females were dissected within 72 hours and the ventral receptacles were examined for the presence or absence of sperm.

Adaptive values based on relative sexual activities can be calculated either on the basis of the number of females inseminated within a certain time or on the basis of the percentage of females inseminated. Fortunately the two methods give quite similar results. The use of the number of females inseminated follows from the assumption that a male can inseminate a certain number of females; if fewer than this number are available, all will be inseminated; if more than this number are present, the excess will be uninseminated. Calculating on the basis of the percentage of females inseminated, on the other hand, implies that a male's sexual capacity increases with the number of females available to him. Actually, there must be a limit to the capacity of any male but, even in the presence of fewer females than his limit, the probability of meeting and courting a receptive female decreases steadily as the number of non-virgin females increases. This causes the fraction of females inseminated to fall short of 100% in a test which runs for a limited time only. The correct adaptive value, then, lies somewhere between the values obtained by the two methods of calculation.

If the activity of ST males is represented by 1, the activity of SR males (x) is either

(1) $x = \frac{aef}{bdc}$ (based on the fraction of females inseminated)

or

(2) $x = \frac{ae}{bd}$ (based on the number of females inseminated)

where a = number of females inseminated by ST males
b = number of ST males
c = total females exposed to ST males
d = number of females inseminated by SR males
e = number of SR males
f = total females exposed to SR males.

Since adaptive values in this case depend directly upon activity, the figures obtained from these calculations can be accepted as estimates of adaptive values.

The results of sexual activity tests both at 25° C. and 16½° C. are given in table 13. The adaptive value for ST males is in all cases equal to 1; the value for SR males at 25° C. is either .820 or .788 depending upon the method of calculation, at 16½° C. either .878 or .846. SR, then, lowers the sexual activity of males which carry it and, therefore, selection affecting the relative frequencies of ST and SR in populations acts through the sexual activity of males as it has in the factors studied previously.

The present experiment was designed to test not only sexual activity but also sexual preference, a phenomenon quite as interesting but completely independent. It will be recalled that two types of females (marked by clipped wings) were exposed to the males in each test. This technique, known as "multiple choice," has been used extensively to detect sexual preference between individuals of different species, races, and mutant types. The important considerations in the present case are these: in each run (e.g., five vials of ST males with SR/SR and SR/ST females and five vials of SR males with SR/SR and SR/ST females) the two types of males were of identical age; the two types of females were not always of the same age; females of any one type, however, were alike in age and were divided equally but arbitrarily between the two types of males. Since the choice offered to one type of male was identical with that offered to the other, the distribution of inseminations between the two types of females should be the same for both males. A significantly different distribution of inseminations by the two males indicates that the genotype of the female is influencing the preference of one or both males. (Ascribing the "preference" to the males is a figure of speech since either or both sexes may be responsible.)

The distributions of inseminations obtained at both 25° C. and 16½° C. are given in table 14. An analysis of the data by means of a $2 \times 2 \times 2$ table (Snedecor, 1946, section 9.8) reveals that the two types of males react differently to the two types of females when the choice of females involves SR/ST and ST/ST at 25° C. or SR/SR and SR/ST at 16½° C. The probability that the distribution obtained for each of these choices is the result of sampling errors is less than .05. The observed distribution of inseminations between SR/SR and SR/ST and SR/SR and ST/ST at 25° C. each has a probability of .05–.08; although not significant, these results suggest very strongly that sexual preferences exist.

Hogben (1946) discusses the effect of non-assortative mating on gene frequencies; the effect depends not only on the degree of preference but also on the gene frequencies themselves. Since the adaptive value assigned to any phase of the life cycle reflects the influence that phase has on gene frequencies, it follows that an

TABLE 13. *Sexual activity of males.* Selective values have been computed (1) with and (2) without an allowance for the number of females tested

	Genotype of male	Number of males tested	Number of females dissected	Number of females inseminated	Selective values	
					(1)	(2)
25° C.	ST	273	508	283	1	1
	SR	284	488	232	.820	.788
16½° C.	ST	275	561	407	1	1
	SR	254	541	318	.878	.846

TABLE 14. *The distribution of inseminations by the two types of males between females of different genotypes.* Inseminations are indicated by +; non-inseminations by −

	Male	Female					
		+	−	%+	+	−	%+
25° C.		SR/SR			SR/ST		
	SR	42	24	63.64	26	52	33.33
	ST	32	42	43.24	28	47	37.33
		P = .06 − .07					
		ST/ST			SR/ST		
	SR	39	48	44.83	59	37	61.46
	ST	51	40	56.04	45	47	48.91
		P = .03 − .04					
		SR/SR			ST/ST		
	SR	28	58	32.56	38	47	44.71
	ST	49	36	57.65	78	13	85.71
		P = .08					
16½° C.		SR/SR			SR/ST		
	SR	41	38	51.90	31	50	38.27
	ST	56	27	67.47	66	19	77.65
		P = .04 − .05					
		ST/ST			SR/ST		
	SR	61	36	62.89	83	25	76.85
	ST	82	31	72.57	85	23	78.70
		P = .50 − .60					
		SR/SR			ST/ST		
	SR	58	30	65.91	44	44	50.00
	ST	71	13	84.52	47	41	53.41
		P = .06 − .07					

adaptive value assigned to sexual preference would have to include a consideration of gene (in this case, chromosome) frequencies. For this reason, sexual preferences will be ignored as agents influencing the frequency of SR in populations.

5. *Egg hatchability*

The detailed analyses were originally intended to determine whether or not selection acted at any of several stages during the life cycle of the fly. Although it was admittedly impossible to study all factors through which selection could operate, the investigation was intended to be as complete as possible. At a rather late date it was realized that the sequence of analyses covered the life cycle from the hatching of eggs until oviposition but that no data had been collected on the hatchability of the eggs laid by the different females.

The technique for obtaining data on hatchability consisted of saving spoons of eggs from the fecundity experiments and counting the unhatched eggs after 48 and 72 hours for the warm room and 72 and 96 hours for the cold room. There was such a small decrease in the number of unhatched eggs between the first and second counts of the early tests that the second count was discontinued. To summarize, then, spoons were exposed to females at 0 hours, counts for fecundity were made at 24 hours, and counts for hatchability were made at 48 hours at 25° C. and at 72 hours at 16½° C. The numbers of eggs studied for each type of female at the start of every experiment were kept at approximately 100 by trimming excess eggs and food from the spoons with a scalpel. The eggs that were retained were always undisturbed.

Several considerations should be noted

in connection with this experiment. First, the zygotic constitutions of eggs laid by females of different genotypes were not the same. Since the females were kept with ST males at all times, SR/SR females were laying eggs of two types, SR/ST females and SR males; SR/ST females laid eggs of four types, SR/ST and ST/ST females and SR and ST males; and ST/ST females laid eggs of two types, ST/ST females and ST males. If the hatchability of an egg depends upon both maternal effect and upon the genetic constitution of the egg itself (or an interaction between the two), then the data presented below must be regarded as approximate. Secondly, this experiment was carried out during the last half of the 25° C. fecundity experiments when all the females were past their peak of productivity. Robertson and Sang (1944) report that egg hatchability decreases as the females increase in age and it may be possible that the females in this case were at different physiological ages although chronologically they were identical. However, it must be remembered that the females being tested were raised in population cages, not in culture bottles. Robertson and Sang report in another section of their paper that starvation during larval life effects egg mortality. The 90% mortality which occurs during the larval stage in a food cup in a population cage, and which has been shown to be differential among the zygotic types, might be expected to be reflected in a differential mortality of the eggs deposited by "cage" flies.

TABLE 15. *Hatchability of eggs deposited by females of different genotypes.* All females were inseminated by ST males

	Genotype of female	Eggs tested	Eggs hatched	Per cent hatched	Relative hatchability
25° C.	SR/SR	317	66	20.8	.234
	SR/ST	461	410	88.9	1
	ST/ST	479	257	53.7	.603
16½° C.	SR/SR	579	418	72.2	1.000
	SR/ST	562	399	71.0	1
	ST/ST	606	414	68.3	1.000

Table 15 gives the results of the hatchability experiments. The differences at 25° C. are very large; only the differences found during larval competition are larger. At 16½° C., where differences in general have been relatively small, there is no difference between the different females in the percentage of eggs which hatch. This is the only analysis made in which the three types of females gave results which did not differ significantly.

6. *Estimation of adaptive values*

In the last several sections we have considered various phases of the life cycle for which the adaptive values of individuals of different chromosomal constitution could be obtained experimentally. The role played in the process of selection by some of the factors studied is obscure (sexual preference or sexual activity of females, unanalysed in the text) or variable (longevity without food and, again, sexual preference). It seems proper at this time to attempt to estimate the combined effects of the variables studied.

An understanding of the nature of the process of selection must precede attempts to evaluate the importance of combinations of selective differentials. The values obtained for the differential survival of the three types of females at 25° C., as established by the experiment on larval competition, are: SR/SR, .152; SR/ST, 1; and ST/ST, .847. These figures tell us that a population consisting initially of equal numbers of freshly hatched larvae of each type living under the conditions of a population cage would yield 152 adult SR/SR females for every 1000 SR/ST females and for every 847 ST/ST females. The values obtained from relative longevities of adults tell us that adult SR/SR females live, on the average, only .645 as long as SR/ST or ST/ST females. The flies which are least resistant in larval competition are also the most short-lived ones. 152 SR/SR females live only .645 as many

fly-days as 152 SR/ST or ST/ST females; 152 SR/SR females live only .152 × .645 or .098 as many fly-days as 1000 SR/ST females. ST/ST females, on the other hand, live as long as SR/ST females, but since only 847 survive the larval competition for every 1000 of the latter, ST/ST females aggregate, .847 × 1.000 or .847 as many fly-days as SR/ST females. Clearly, then, the advantages and disadvantages of the chromosomal types at the different stages must be multiplied in order to obtain the values which take into account the differences at all phases of the life cycle. These final values are estimates of the various degrees to which the composition of successive gene pools is influenced by flies of different chromosomal constitutions.

For several variables studied, the estimates of the effects on the genetic constitution of populations depend upon the method of computation. This is true for the sexual activity of the males and for the fecundity of females. Either of the alternate values may be chosen for the final computation. In the case of the males it makes relatively little difference which value is chosen and it is probable that the true value is intermediate. In the case of females, where the difference is more pronounced, it still makes little difference which values are chosen; the most divergent values were used in computing table 16.

In table 16, the various adaptive values have been assembled for comparison. In the overall figures it is obvious that at 25° C. the adaptive value of the heterozygous females is higher than that of the two homozygous females and that the ST males surpass SR males. This situation

TABLE 16. *Summary of adaptive values for various phases of the life cycle*

	Males		Females		
	SR	ST	SR/SR	SR/ST	ST/ST
25° C.					
Larval competition	.407	1	.152	1	.847
Longevity w/food	1.086	1	.645	1	1.000
Fecundity*	—	—	.627	1	.615
Fecundity**	—	—	.580	1	.543
Sexual activity†	.820	1	—	—	—
Sexual activity††	.788	1	—	—	—
"Sex-ratio"	2.000	1	—	—	—
Egg hatchability	—	—	.234	1	.603
Overall selective value					
Maximum	.724	1	.021	1	.314
Minimum	.696	1	.014	1	.277
16½° C.					
Larval competition	.740	1	.622	1	.940
Longevity w/food	1.113	1	.819	1	1.000
Fecundity*	—	—	.545	1	.903
Fecundity**	—	—	.552	1	.781
Sexual activity†	.878	1	—	—	—
Sexual activity††	.846	1	—	—	—
"Sex-ratio"	2.000	1	—	—	—
Egg hatchability	—	—	1.000	1	1.000
Overall selective value					
Maximum	1.452	1	.343	1	.849
Minimum	1.393	1	.278	1	.734

* Eggs/female (average of all counts). ** Total eggs/original number females.
† Using fraction of females inseminated. †† Using number of females inseminated.

obtains at 16½° C. also, except that the SR males, largely by virtue of the "sex-ratio" effect, now surpass the ST males; at 25° C. SR males were inferior in spite of this effect. The differences between the three types of females are less pronounced at 16½° C. than at 25° C. When the adaptive values of different variables are compared, they are seen to vary considerably. SR males, which do very poorly in larval competition at 25° C., have a slightly longer adult life than ST males but are less active sexually. Values for SR/SR females (at 25° C.) range from .152 to .645 while those for ST/ST females range from .543 to 1.000.

We now have two sets of data which have been obtained independently but which may be compared. One set consists of the estimates of the adaptive values of flies of different chromosomal constitutions, the other consists of data on the changes occurring with time in chromosomal frequencies in populations living in population cages. Exact comparison is hindered by the following circumstances. First, our analyses were concerned with only the most obvious physiological factors through which selection could act. We have already mentioned our ignorance concerning the importance of surviving in the absence of food and of sexual activity of females. Complexities introduced into the problem by variable sexual preferences have been ignored. It is possible to imagine other factors which were overlooked or were too difficult to study experimentally: the amount of sperm deposited during copulation by different males; the efficiency with which different females utilize sperm; differential ability of males to copulate with non-virgin as opposed to virgin females; and the ratio of the larval to the total life span. Genotypic differences in these additional factors would also have selective importance. Second, the conditions under which our analyses were made were not "cage" conditions. Longevity was determined in bottles (with food) or in vials (without food), sexual activity in clean vials, fecundity in vials with spoons of food, and egg hatchability in vials. It is known that population density, for instance, affects longevity (Pearl, Miner and Parker, 1927) and fecundity (Pearl, 1932). It would be a mere accident if the correct population density was chosen for any of the experiments performed. In addition to population density there is the problem of the effect of the presence of food on the receptiveness of females or on the activity of males. The humidity, which has been found to affect differentially flies carrying different arrangements of the third chromosome (Heuts, 1947), varies in a population cage from nearly 100% on the surface of the food to 70–80% on the wire screen on the sides of the cages; in the analyses, humidity was uncontrolled but was probably nearly 100% in all containers with food. In the longevity tests without food the humidity was kept at 92% by the concentrated NaCl solution.

Discussion and Conclusions

The results obtained in the population cages show that, in competition with ST, SR decreased in frequency; but, whereas SR was eliminated at 25° C., it was retained in populations at 16½° C. Analyses of physiological properties of flies differing in their chromosomal constitutions furnish an explanation for these changes: at 25° C. the adaptive value of SR/SR females is close to zero; hence, their contribution to the gametic pool of the population is extremely limited; SR males contribute less than ST males. The superiority of SR/ST females at 25° C. tends to establish an equilibrium but the inferiority of SR/SR females and of SR males is sufficient to upset this tendency and to result in the elimination of SR from the population. At 16½° C., on the other hand, the contribution of SR males to the gametic pool is higher than that of ST males. The adaptive value of SR/SR females, although low, is substantially greater than zero. Conse-

quently, SR is retained in populations at this temperature. The adaptive values estimated from the physiological experiments cannot be regarded as anything more than rough approximations to the values obtaining in the population cages; nevertheless, the orders of magnitude at each temperature and the differences in magnitude between the two temperatures are such that the changes occurring in the population cages are adequately explained on the basis of selection.

The demonstration of selective forces operating within the experimental populations supports the hypothesis that the geographical distribution of SR in natural populations of *Drosophila pseudoobscura* (see page 192) is also the result of natural selection. In the experimental populations SR was eliminated at 25° C., while an equilibrium with ST was established at 16½° C. Populations from that part of the geographic range of *D. pseudoobscura* in which SR occurs resemble those in the population cages kept at 16½° C., while the natural populations which lack SR are similar to the experimental populations kept at 25° C. The gradients observed in the frequency of SR in the natural populations reflect gradients existing in environmental conditions which govern the adaptive values of flies of different genotypes; the seasonal fluctuations (see page 191) are the result of local, temporary variations of these conditions. Obviously, more than temperature is involved in the determination of points of equilibria in natural populations (and, hence, the distribution pattern) of SR, because SR reaches its maximum frequency in one of the warmest regions of the United States and is absent in the cooler regions. On the contrary, in the experimental populations SR was eliminated at the higher of the two temperatures. This apparent discrepancy is probably the result of the interaction of many environmental agencies in the determination of the adaptive values of the different types of flies in natural populations.

The geographical distribution of SR based upon gradients of equilibria established by natural selection does not exclude the possibility that a further spread, or a contraction, of the distribution of SR will occur; SR will increase or decrease its range if the relative adaptive values of SR males, SR/SR females, or SR/ST females increase or decrease either because of changing environmental conditions or because of new gene mutations. The "sex-ratio" effect inherent in SR (see Introduction) has been transcended by larger selective forces; consequently, this effect will be only one of many factors concerned with any future change in the distribution of SR.

The relative magnitudes of the adaptive values of the various chromosomal types established by the physiological analyses merit consideration. ST males have adaptive values 1.3 (25° C.) and .7 (16½° C.) those of SR males; ST/ST females have adaptive values 15 (25° C.) and ca. 2 (16½° C.) those of SR/SR females. SR/ST females are superior to either of the other types of females at both temperatures, markedly so at 25° C. It appears as if genes are present on the X-chromosome which are sex-limited in their action (indeed, sr affects meiosis in males only) or else the relation between the adaptive values of ST and SR males would have been similar to the relation between the adaptive values of ST/ST and SR/SR females. Such genes, if limited in action to females, will respond to selective forces like autosomal genes, i.e., if recessive, they will increase in frequency in populations until females carrying them in the homozygous condition are formed. The superiority of heterozygous females (SR/ST) might result from an inter-allelic reaction which results specifically in an increased adaptive value of SR/ST females. Crow (1947) has shown that it is probable that, in a cross-breeding population, dominance can account for only a small increase in the survival value of heterozygotes whereas allelic interaction can account for much

larger increases; the marked superiority of SR/ST females in the present studies would indicate that an allelic interaction is operative in the present case.

It is interesting, in closing, to determine whether "sex-ratio" presents a unique situation in problems of population genetics and natural selection. In short, SR (because of the "sex-ratio" condition) possesses a great inherent selective advantage over ST but is prevented from replacing ST in populations because of the extremely low adaptive value of SR/SR females. The retention of SR, in fact, seems to depend as much upon the superiority of SR/ST females as upon the "sex-ratio" effect. If SR is to present a unique situation, the responsible factor should be either the superiority of heterozygous females or the inherent selective advantage of SR.

The superiority of SR/ST females certainly is not uncommon. Wright and Dobzhansky (1946) have shown that a number of arrangements of the third chromosome of *D. pseudoobscura* form heterozygous individuals which are superior to individuals homozygous for any one arrangement. The arrangements of the third chromosome which were studied were Standard, Arrowhead, and Chiricahua: equilibria resulted in populations at 25° C. when any two or all three chromosomal arrangements were present. Dobzhansky (1947) subsequently obtained evidence that the equilibria obtained were actually the result of heterozygote superiority during the larval stage.

Cases, other than "sex-ratio," are also known in which genes possess inherent selective advantages, i.e., genes which tend to increase in frequency independently of any effect on the viability or survival of individuals which carry them. Patterson (1946) states that the gene(s) responsible for the insemination reaction in numerous species of *Drosophila* should automatically increase in frequency in populations. This increase should result from the frequent refusal of females which have experienced the insemination reaction to mate again during their lifetimes. The sperm of males which evoke this reaction, consequently, will be the only sperm to fertilize the eggs of these females; ordinarily, because of re-inseminations, sperm of several males are used to fertilize the eggs of any one female. In *Primula vulgaris* there exist allelic genes which cause plants to have different kinds of flowers designated as pin, thrum, and long homostyle; the pin and thrum types are self sterile but are interfertile, plants with long homostylic flowers are self fertile as well as interfertile. The increased possibilities of fertilizations of the long homostylic type should favor the spread of the "long" allele in populations; that this spread is actually occurring is indicated by the replacement of pin and thrum types by the long homostyle type in two areas studied (Catcheside, 1947, and oral communication).

Summary

"Sex-ratio" (sr) is a sex-linked genetic condition which occurs in several species of *Drosophila*. In *D. pseudoobscura*, sr causes an elimination of the Y-chromosome and an additional division of the X-chromosome during spermatogenesis; consequently, sr males produce only X bearing sperm and have progenies consisting only of females. Since these males introduce twice as many X-chromosomes into populations as normal males, X-chromosomes carrying sr are expected to replace the normal X-chromosomes.

In *D. pseudoobscura* X-chromosomes which carry "sex-ratio" (SR) differ cytologically from the standard (ST) X-chromosomes by three inversions.

Seasonal fluctuations in the frequency of SR in natural populations indicate that natural selection prevents SR from replacing ST; the geographical distribution is consistent with the hypothesis that selection results in gradients of equilibria extending in all directions from the region of highest frequency of SR (ca. 30%) in southern Arizona and northern Mexico.

Experimental populations containing

high (75% in females, 50% in males) and low (25% in females, 50% in males) initial frequencies of SR were studied at 25° C. and 16½° C. The frequency of SR decreased with time in all populations; at 25° C., ST reached 100% in 210 days; at 16½° C., ST had increased to 90–94% after 420 days and apparently reached an equilibrium. Changes which occurred during the course of these experiments can be accounted for on the hypothesis that the relative frequencies of SR and ST are determined by natural selection.

Several phases of the life cycle were studied to determine the nature of the selective forces which might be involved: differential survival during the larval stage, longevity of adults, fecundity, sexual activity, and egg hatchability. Flies of different chromosomal constitutions differ in nearly all of these respects. Estimates of the adaptive values based on the results of these analyses indicate that, at 25° C., SR males are inferior to ST males, SR/ST females surpass by far either of the other types of females, and ST/ST females are superior to SR/SR females whose adaptive value is close to zero. At 16½° C., SR males surpass ST males and SR/ST females are superior to SR/SR and ST/ST females. However, at 16½° C., ST/ST females are only slightly inferior to SR/ST females; SR/SR females are markedly inferior. (See table 16 for a summary of data.) The results of these analyses are sufficient to explain the changes observed in the experimental populations.

It is suggested that selective forces analogous to those operating in the experimental populations can adequately account for the geographical distribution of SR in *D. pseudoobscura*.

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HISTOLOGICAL CHANGES CORRELATED WITH EVOLUTIONARY CHANGES OF BODY SIZE

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1. ALLOMETRY IN EMBRYOLOGY AND IN EVOLUTION

Nearly all evolutionary changes of species are accompanied by changes in body size. In very many cases a successive enlargement of body size takes place in phylogeny, a phenomenon known as Cope's Rule. This rule holds good especially for vertebrates, but for many groups of invertebrates as well (Cope, 1884, 1896; Dépérét, 1907; Rensch, 1943, 1947). In other cases, chiefly among small insects, reductions of body size have taken place during evolution and are correlated with the reduction of certain normal structures, e.g., the wing veins. But in whatever direction the changes of body size occur, they are accompanied by alterations in the proportions of some organs and structures. This fact was partly known to G. Galilei (1618, p. 559). It was confirmed by B. Robinson (1748) with regard to the relative size of the heart, and by A. von Haller (1762) with regard to the relative size of the brain and eyes. These are organs that become relatively smaller with increasing body size. C. Bergmann (1847, 1852) gave a causal explanation of these changes of proportions by pointing out that organs which function as surfaces (such as epidermis, intestine, lungs) increase in growing organisms as the square, while the bulk of the body is cubed. Recently these problems were thoroughly analyzed by D'Arcy Thompson (1917), Klatt and Vorsteher (1923) and especially by J. Huxley (1932). Following Huxley we now speak of positive allometric growth when an organ grows more rapidly than the whole body, and of negative allometric growth when it grows more slowly. During the postnatal development of a bird, the growth of brain and eyes, for instance, is negatively allometric, i.e., at birth they are relatively much larger than in adulthood, whereas the growth of bills and legs is positively allometric.

The proportion of an organ to the rest of the body may thus shift allometrically either during ontogeny or during phylogeny. If definite growth gradients are inherited, an increase of body size in a line of descent must be accompanied by large alterations in the proportions of parts of the body. Many orthogenetic changes of organs and many excessive characters can thus be interpreted (Huxley, 1932), provided there is a selective advantage in a steady alteration of body size. I believe I have shown the great probability of such a directed selection in lines of descent showing increasing body size (Rensch, 1947). It seems to be of great importance to point out that natural selection often acts primarily on body size and only secondarily on single organs. As a consequence, the proportions of the organs are changed. In cases of great size differences this may lead to a transformation of the structure of the whole body. It is therefore very important to study allometric growth in all groups of animals during ontogeny as well as phylogeny. Studies of growth gradients during ontogeny were made especially by J. Huxley and his school, first with the carapace and legs of Crustacea but later with many other characters of animals and plants. Though these embryological investigations have yielded copious quantitative data, they consist so far only of selected examples which show the applicability of the principle of allo-

metry to various morphological and physiological researches. Eventually, however, all characters utilized in embryological, evolutionary, and taxonomic research will need such an analysis.

When applying the rules of allometry to a phylogenetic problem, it must be carefully determined in each case if the evolutionary change of size is caused merely by a prolongation or abbreviation of ontogenetic development. According to my experience, shifts in proportions are not always produced in this manner. The relative length of intestine among homoeothermal animals, for instance, is greater in larger than in related smaller species (of corresponding habits), although growth of the intestine is negatively allometric during the last postnatal phase (Rensch, in press). Furthermore, the hairs of mammals and the feathers of birds are relatively shorter (at the same season) in large species than in related smaller ones, although in these cases characters of marked positive allometry are involved. Also, hairs of larger rodents, like rats, consist of several rows of cells, whereas hairs of mice have only a single row. This also shows that the hairs of rats cannot be considered merely as allometrically enlarged hairs of mice. Thus, not all phylogenetic changes of size occur along allometric gradients.

It has been shown, moreover (Rensch, 1947, p. 140), that the curves which represent the growth gradients of large species in a system of coordinates are not simply the continuation of the curves of related small species (as would have to be the case if the growth ratios remained constant). Rather, they run parallel or even form different (in smaller species mostly steeper) angles with the abscissa. In such cases, therefore, only the allometric trend remains the same (e.g., negatively allometric). The available data indicate the general rule that large species are not merely allometric alterations of related smaller species. It appears therefore certain that natural selection controls not only body size as a whole but also individual growth gradients. When analyzing evolutionary changes of body size, we must determine for each organ the portion of the change that is due to allometric growth, and the portion that is due to special selective factors.

Theoretically, there exist several possibilities. (1) The growth ratios may have remained constant during the evolutionary change of body size, but those variants which begin with a higher initial value (e.g., with a larger first *anlage* of the organ) have been preserved by natural selection (fig. 1A). (2) The allometric trend may be altered, that is to say, a positively allometric growth gradient may ascend more steeply (fig. 1C), or a negatively allometric growth gradient may drop more slowly (fig. 1B). (3) While the allometric conditions of the last postnatal period of growth may remain the same (e.g., negative allometry), this period may be preceded by a prolongation or an intensification of an earlier period of positive allometric growth (fig. 1D). It is well known that in many growing organs a repeated change of positive and negative allometry takes place during development. This third case with its different variations seems to be common, as many organs show periods of accelerated

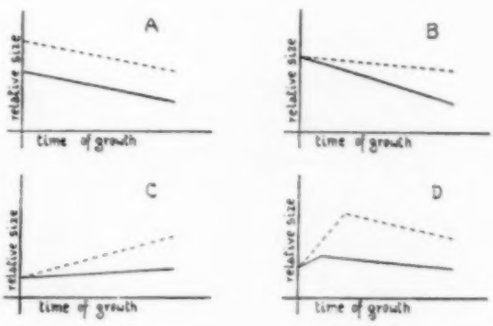

FIG. 1. Four different possibilities of embryological changes which result in the same relative enlargement of an organ. Solid line: curve of allometric growth (e.g., organ in per cent of body size) of the ancestor; dotted line: of the enlarged descendant. A. Increased initial size. B. Decrease of negatively allometric growth. C. Increase of positively allometric growth. D. Increase only of initial period of positively allometric growth.

embryonic growth. For instance, the eyes and the nervous apparatus connected with them show accelerated growth shortly before the young animal opens the eyes. The relative length and intensity of this period may have a greater effect on final size than the subsequent negatively allometric period. (4) Finally, the above mentioned three possibilities may be combined in various ways. A causal analysis of evolutionary variations in growth requires therefore detailed embryological researches.

Further questions arise in applying the principle of allometry to histological structures of related species of different body size. It is to be expected that tissue structure too will change markedly owing to the interaction of gradients of different rates of growth, and that this may lead to a decided change in the function of an organ. The present paper consists of a short presentation of three problems from this field, the study of which we have begun in the Zoological Institute of the University of Münster: (1) the (largely) allometrically caused formation of new histological structures in species with enlarged body size, (2) the reduction of histological structures to the indispensable components when body size is reduced to the lower evolutionary limit, and (3) the alterations of structure, taking place in very small species in order to compensate for other disadvantages of structure. The following account is based primarily on the investigations of three of my students: W. Partmann, H. Goossen, and K. W. Harde. Some of these problems have been treated already in my recent book (Rensch, 1947).

2. Change of Histological Structure Correlated with Evolutionary Increase of Body Size

In the case of so-called permanent tissues ("Dauergewebe"), the differences between closely related large and small species are due to differences in cell size and not to changes in cell number. In these cases the cells lose their capacity for division early with the result that there often exists a constancy of cell number (eutely), e.g., in a ganglion. In extremely large animals this results in the production of giant nerve cells with a peculiar lobulated, fenestrated or sponge-like outer zone (so-called paraphytes), as described by G. Levi (1925). On the contrary, in tissues in which the cells continue to divide, the difference in the size of cells between large and small species is usually insignificant. In these

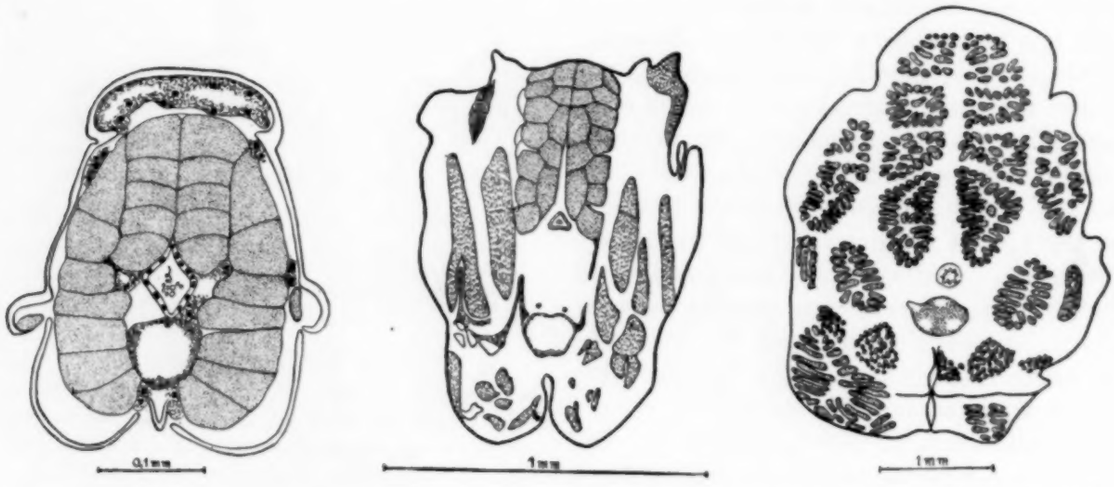

Fig. 2. Homologous transverse sections through the thorax of three Nematocera (Diptera) of different sizes showing the change of structure in the flight muscles (dotted). (Ventral cord of the nervous system coarsely dotted, light inside.) Left, *Contarinia* spec.; middle, *Culex pipiens;* right, *Ctenophora atrata* (after Partmann).

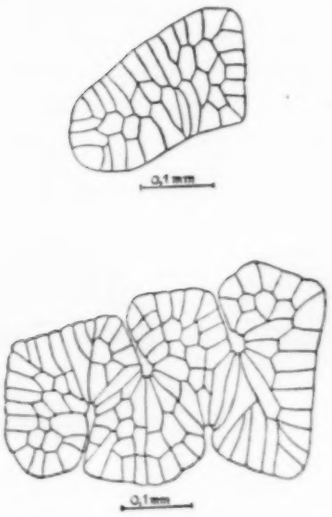

FIG. 3. Transverse sections of the second dorsal longitudinal muscle in two Cyclorapha (Diptera) of different sizes. Upper: *Musca domestica;* lower: *Eristalomyia tenax* with intramuscular folds (after Partmann).

instances the organs differ principally in the number of cells.

Flight Muscles

If certain tissues of small animals are composed of relatively few cells, an increase in the number of cells occasionally alters the possibilities of providing these tissues with nutriment and oxygen. This is particularly the case with the flight muscles of insects. In this group of animals, in which a closed system of blood vessels is absent, too great an increase in the number of muscle fibers would produce compact bundles, the inner parts of which could not be nourished efficiently. In larger species therefore a new histological structure is developed; the flight muscles lose their compact structure and are divided into many bundles. This is illustrated in figure 2 by homologous transverse sections of three Nematocera (Diptera) of different size (based on the work of W. Partmann). The minute gall-midge *Contarinia* (1.5 mm. long) has compact musculature in comparison to the mosquito *Culex* and the large crane-fly *Ctenophora* (29.5 mm. long), both of which show a strong parcelling of the muscle fibers. In the figure the transverse sections of the three different sized species of Diptera are shown at equal size. Actually the individual muscle packages of *Ctenophora* are larger than those of *Contarinia.* Among other flies Partmann found similar conditions, but in the large species *Eristalomyia,* for instance, the individual muscle packages are loosened up in a very different manner by the development of a novel and hitherto not yet ob-

FIG. 4. Transverse sections through homologous parts of the mid-intestine in Dytiscidae of different sizes. Left: *Laccophilus obscurus;* right: *Dytiscus marginalis.*

served type of structure. The muscles are folded into a series of longitudinal pleats between which branches of the tracheal system enter (fig. 3).

Intestinal Cells

The intestine of the Diptera follows a rule which is valid for all animals; in large animals it is not only absolutely but also relatively longer than in small animals. Except for those Nematocera (Diptera) that have a straight intestine, this lengthening is combined with an increase in the number of loops (W. Partmann), the origin of which can be traced to special growth centers. Furthermore, the surface of the intestine is increased in large insects by the formation of more folds in the intestinal wall. Figure 4 shows this difference between a large and small species of Dytiscidae (water beetles). To facilitate comparison the transverse sections are drawn at equal size. In this manner the cell nuclei of the large *Dytiscus* are reduced to points, but it can easily be seen that the interior surface of the intestine is divided by many fine folds, whereas in the small *Laccophilus* the lumen shows only a few coarse folds.

This difference is, in part, caused by the fact that the intestinal cells are long cylindrical or club-shaped in the large beetle, whereas those of the small species are nearly cube shaped (fig. 5). The same difference occurs between the cells of the mid-intestinal glands (fig. 6), which are attached to the intestine like prominent humps or tubes. The number of glands of the middle intestine is much higher in the large species than in the small one; figure 4 shows in the former case 64, in the latter case only 8 sectioned gland tubes. The marked elongation of the cell form of large species can also be

FIG. 6. Transverse sections through the glands of the mid-intestine in Dytiscidae of different sizes. Left: *Laccophilus obscurus;* right: *Dytiscus marginalis.*

seen if we compare two related beetles of the family of Scarabaeidae: the large *Geotrupes stercorosus* (10–16 mm. long) has cells of a similar slender form to those of the large water beetle in its middle intestine, the small *Melanipterus punctatosulcatus* (4–6.2 mm. long), on the other hand, has stouter intestinal cells. This rule of folds and of cell form is equally valid among the Diptera according to W. Partmann's investigations. The small dark-winged fungus gnat *Lycoria* shows cuboid cells in the middle intestine, whereas the large mosquito *Theobaldia* has cylindrical cells and some folds. Still smaller insects, such as the minute gall-midge *Contarinia* (1.5 mm. long) and even more markedly the aphid *Phoradon persicae* (fig. 7), have in general only

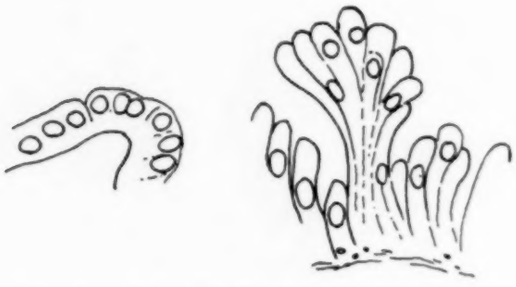

FIG. 5. Cells of the mid-intestine of two Dytiscidae of different sizes. Left: *Laccophilus obscurus;* right: *Dytiscus marginalis.*

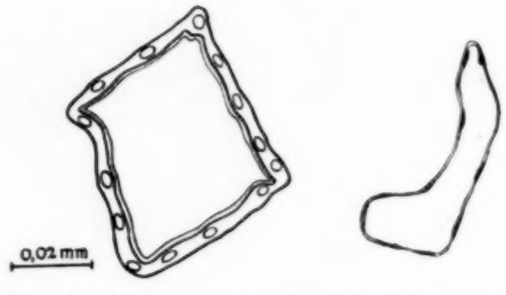

FIG. 7. Transverse sections through the anterior mid-intestine of very small insects. Left: gall-midge *Contarinia* spec. (after Partmann); right: aphid *Phoradon persicae.*

pavement epithelium in the middle intestine.

Since the ontogenetic development of the intestinal epithelium begins with flat or cubic cells which tend later to attain cylindric shape, the assumption is obvious that development is terminated precociously in very small species (Partmann). And conversely, since a special growth gradient is actively stretching the intestinal cells in a longitudinal direction, the evolutionary increase in size of an insect produces very slender cells, and the epithelium and the glands of the middle intestine become thus quite another type of structure. Evolution in such cases represents an "addition to the final stages," an "anaboly" in the sense of Sewertzoff (1931). [The longitudinal direction of growth is probably affected mechanically by the mutual pressure of the neighboring cells.]

The Nervous System in Insects

Of special importance are the changes of histological structure in the central nervous systems. Here again the same rule is apparently valid for the whole animal kingdom. In all groups (with similar modes of life) the large species have relatively smaller brains than related smaller species. This has long been known for vertebrates as Haller's Rule, but H. Goossen has recently pointed out that the same correlation is valid for insects. For example, the cockchafer *Melolontha vulgaris* (body length 23 mm.) has a brain weight of 5 per mille of the body weight. In the related but smaller beetle *Phyllopertha horticola* (body length 9.2 mm.) the brain weight is 28.8 per mille of the body weight. The larger brains also show different proportions. They are less compact and the optic lobes are relatively more slender and longer. Since in larger species the brain occupies less space in the head capsule, the optic lobes are extended in a nearly straight line, whereas in small species they are stouter and form an angle (fig. 8). The three optic masses (lamina ganglionaris, medulla externa, and medulla interna), which are in close proximity in small species, move apart in larger species. In the small aphid *Phoradon persicae* they are especially tightly pressed together.

The most pronounced histological

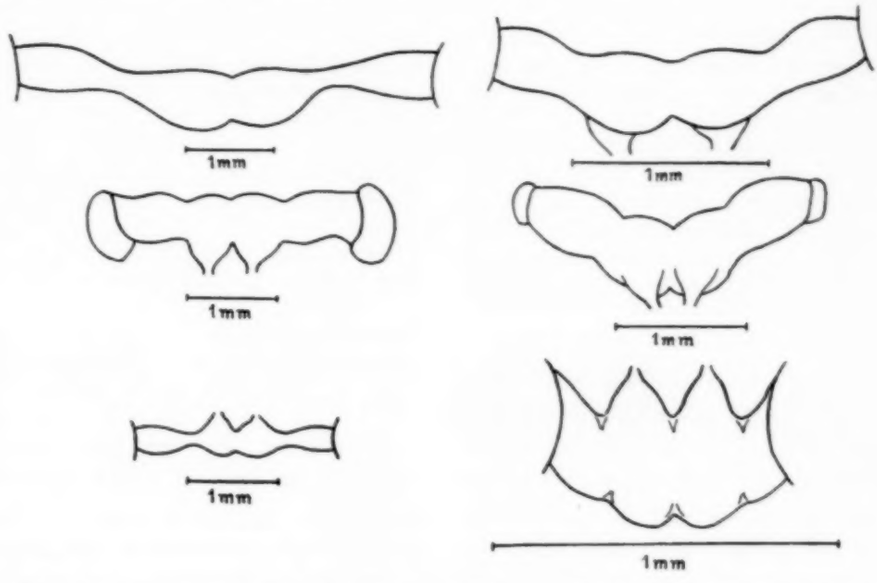

FIG. 8. Shape of brains in beetles of different sizes. Pairs of species of the same family. Large sized species on the left. Above, Dytiscidae: left, *Dytiscus marginalis;* right, *Ilybius fenestratus.* Middle, Scarabaeidae: left, *Melolontha vulgaris;* right, *Phyllopertha horticola.* Below, Carabidae: left, *Carabus nemoralis;* right, *Argutor diligens* (after Goossen).

changes are shown by those parts of the brain which among insects are commonly regarded as an index for the degree of complication of the nervous processes and thus for the psychic qualities, namely the corpora pedunculata. As H. Goossen could show, these organs are not only relatively larger in large species, but the various growth gradients determining their shape must have also a different rate, for the corpora pedunculata of large species are much more differentiated and

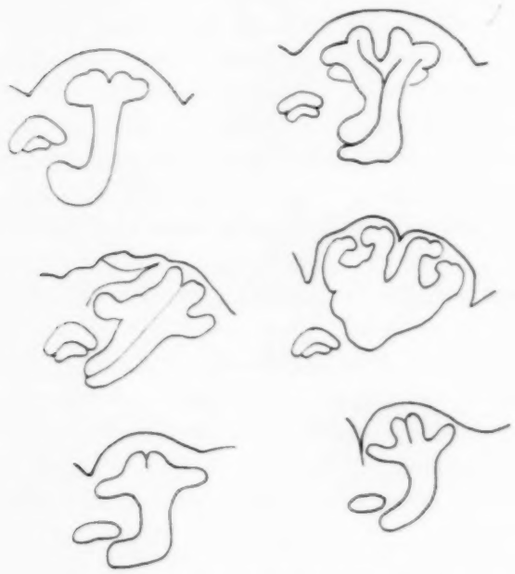

FIG. 9. Maximum sections through the corpora pedunculata and the central bodies of different sized insects of three families. Above, Scarabaeidae: left, *Phyllopertha horticola;* right, *Melolontha vulgaris.* Middle, Vespidae: left, *Ancristocerus parietinus;* right, *Vespa crabro* (after Goossen, transformed). Below, Blattidae: left, *Blatta orientalis;* right, *Periplaneta americana* (after Bretschneider and Hanström from Goossen).

have a richer surface than those of related smaller species (fig. 9). The much discussed shape differentiations depend therefore not only on the evolutionary level of an insect group, as is generally assumed, but to a considerable degree also on body size. Calculating the upper line of delimitation of the corpora pedunculata (on the largest horizontal sections) in per cent of half the width of the protocerebrum, the following values (after Goossen) are found among comparable large and small species of Coleoptera and Hymenoptera:

TABLE 1

Species pairs	Body length	Relative size of corpora pedunculata
Carabus nemoralis	20.0 mm.	102.0 per cent
Agonum muelleri	6.6 mm.	39.4 per cent
Hydrous piceus	42.4 mm.	93.1 per cent
Hydrophilus caraboides	15.9 mm.	36.5 per cent
Melolontha vulgaris	22.0 mm.	195.8 per cent
Phyllopertha horticola	9.4 mm.	96.6 per cent
Vespa crabro	22.2 mm.	339.0 per cent
Ancristocerus parietinus	6.2 mm.	212.7 per cent

In addition to this enlargement of the surface, there is also an increase in the number of globuli cells. The corpora pedunculata are thus a part of the brain which does not have a constant cell number even during short steps of evolution. This is illustrated by the following figures:

TABLE 2

Species pairs	Body length	Number of nuclei of globuli cells
Dytiscus marginalis	27 mm.	615
Ilybius fenestralis	12 mm.	188
Melolontha vulgaris	20.6 mm.	1176
Phyllopertha horticola	9.9 mm.	624
Vespa crabro	22.2 mm.	1009
Ancristocerus parietinus	7.9 mm.	500
Bombus lapidarius	17.8 mm.	811
Andrena vulgaris	6.2 mm.	545

Finally, it may be mentioned that the size of the central body in the brain of insects is inverse to that of the corpora pedunculata, therefore relatively smaller in large species. Its diameter, calculated in per cent of half the width of the protocerebrum, is, for example, in *Carabus nemoralis* (body length 20.8) 46.3 per cent, in *Agonum muelleri* (body length

6.6 mm.) 56.5 per cent; in *Melolontha vulgaris* (body length 216 mm.) 39.8 per cent, in *Phyllopertha horticola* (body length 9.9 mm.) 45.0 per cent, in *Vespa crabro* (body length 22.2 mm.) 30.8 per cent, in *Ancristocerus parietinus* (body length 6.6 mm.) 36.4 per cent.

The Brain of Vertebrates

Very similar conditions are found in the brain of vertebrates. The pallium of the forebrain is not only absolutely, but also relatively, larger in large species than in related small species, whereas in the latter the other parts, the so-called "brain stem," are relatively larger. Certain histologically definable areas of the cerebral cortex, which are known to have different functions, show a different development. R. Brummelkamp (1940) states that during the individual development of a mammal, such as the sheep, the histologically different areas grow isometrically so that the parts of the cortex do not show any shifting of proportions at different developmental stages of brain size. K. W. Harde of our Zoological Institute came to a different conclusion. He found that in white mice the large, distinctly circumscribed, histologically defined units, as well as also the smaller regions, show very different growth rates. The holocortex 2-stratificatus (function of smelling), for example, shows negatively allometric growth in relation to the cortex of the whole hemisphere up to the tenth day of postnatal development, but then growth becomes positively allometric with an interruption between the twentieth and the fortieth day. The holocortex 5-stratificatus (motor functions), on the contrary, reaches its relative maximum size by the thirteenth day (average day for opening the eyes) and from then growth is negatively allometric in relation to the cortex of the whole hemisphere (fig. 10). The regio praepyriformis and the regio peramygdalaris may be chosen as examples for differences in the allometry of different regions. Calculated in per cent of the whole semicortex, the former region shows a strong positive allometry up to the twentieth day, then a negative allometry. The regio peramygdalaris, on the contrary, has a distinctly negative (although dissimilar) allometry up to the thirteenth day (opening of the eyes) and then grows isometrically (fig. 11).

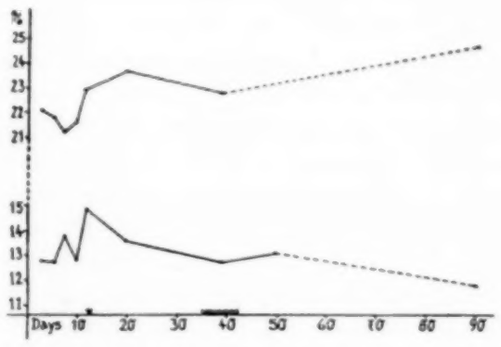

FIG. 10. Differences in growth rates of histologically defined regions in the brain of the white mouse. Relative surface values in per cent of the surface of the whole hemisphere. Upper: of the holocortex 2-stratificatus. Lower: of the holocortex 5-stratificatus. Wedge: day of opening the eyes. Grating: attainment of maturity (after K. W. Harde).

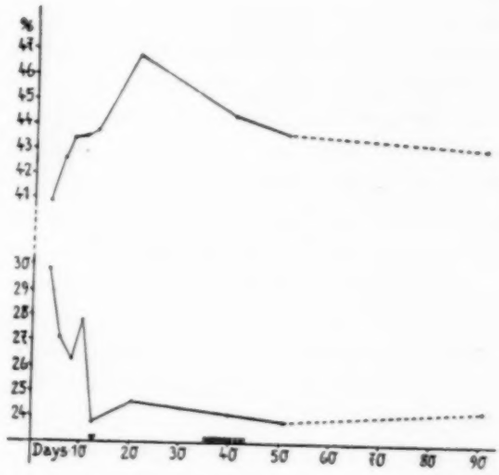

FIG. 11. Differences in growth rates of brain regions in the white mouse. Relative surface values in per cent of the whole semicortex. Upper: of the regio praepyriformis. Lower: of the regio peramygdalaris (after K. W. Harde).

Similar growth rates of the brain regions occur also during evolution, as is evident from a comparison of the relative size of the same histological regions of adult specimens of the mouse, rat, and

rabbit. Most groups of areas of the holocortex 5-stratificatus show—according to the data of Gurewitch et al. (1929)—a relative decrease in the rabbit compared with the rat, and in the rat compared with the mouse, corresponding to the prevailing negative allometry in mice pointed out by K. W. Harde. The areas 4 + 6 + 12 + 23 + 24 added together and calculated in per cent of the whole holocortex 5-stratificatus give the following results: mouse 23.5 per cent, rat 19.0 per cent, rabbit 16.4 per cent. The growth of areas 17 + 18, on the contrary, is positively allometric correlated with body size: mouse 7.1 per cent, rat 8.9 per cent, rabbit 14.5 per cent. A detailed comparison of the individual development of the forebrain of mouse and rat, using the methods of K. W. Harde, is now being undertaken by one of my students (Ch. Schulz). In this way it will be possible to estimate to what extent growth ratios have remained the same and how far evolutionary differentiations have taken place.

In any case, this much is already clear, that an isometrical growth of all histologically circumscribed regions of the forebrain occurs neither during individual development nor during evolution. On the contrary, owing to differences of the growth gradients, a marked alteration in the histological structure of the brain takes place if the body size is enlarged. The hypothesis of E. Dubois (1898, 1930), that the evolutionary increase of the forebrain occurs by jumps, each of which doubles the brain mass, is consequently very improbable.

A modified version of this hypothesis, proposed by Brummelkamp (1939), namely that smaller, so-called $\sqrt{2}$-jumps take place, seems likewise not to be in accord with the above-mentioned results. On the contrary, the alteration of the brain structure during the evolutionary increase occurs in a rather complicated manner and probably in different ways.

These findings on histological alterations of structure encourage speculation on the phylogenetic origin of new parts of the brain, for example, new areas or new regions. A brain region which grows by positive allometry and therefore becomes relatively larger during the evolutionary increase of body size may become larger than its function requires. In that way, brain parts may arise which are available for new functions. Among such additional brain functions are to be mentioned particularly the more complicated associative integrations of the nervous impulses. The so-called associative centers of higher vertebrates may be such positively allometrical parts (although, of course, selection independent of the constant growth ratio may also be effective). Such an enlargement of an area may be accompanied by a new histological differentiation, as we have described above for the corpora pedunculata of insects. I consider it probable that especially the speech center, Broca's region, which has raised man in a decisive manner above the ape stage, may be one of these positively allometrical regions. An investigation of this problem is planned.

3. Reduction to the Indispensable Structures in Very Small Species

If an organism becomes smaller during evolution, this is connected with a reduction in the number of successive cell divisions in tissues the cells of which are permanently capable of division. The cells usually become only slightly smaller or not at all so, but their number becomes greatly reduced. As a consequence, many differentiations and sometimes even whole organs disappear if they are no longer able to function properly on account of their low cell number. This is particularly evident for the male copulatory organ of small land prosobranchs of the large family of Cyclophoridae. The diameter of the shell of most of the snails of this family exceeds one centimeter. A well developed penis is found in all these larger forms. In the small *Moulinsia* species of southeastern Asia (shell length mostly 4–8 mm.) the penis is either rudimentary (*M. pellucidum*) or is lacking entirely (*M.*

floresiana) (Tielecke, 1939). In the still smaller species of *Diplommatina* (e.g., *D. schmidti*) it is likewise lacking. The small marine prosobranch *Caecum glabrum* (shell length 1 mm.) can survive without gills (Götze, 1938), as the diffusion distances are short and the relatively large surface of the foot is sufficient for breathing. Very small Turbellaria have no ramifications of the intestine (Rhabdocoela); very small Cestodes do not show ramifications of the uterus, etc.

In very small insects some segments of the tarsus have usually disappeared. Most larger Coleoptera, Diptera, Hymenoptera, Lepidoptera, etc. have five tarsal segments but the minute Thysanoptera have only one to two, the very small Zoraptera two, the Mallophaga one to two, the Siphunculata only one. Among the beetles the minute Ptiliidae (dwarf beetles, body length 0.25–1.4 mm.) have three tarsal segments, of which the first and the second are only indistinctly separated, and the same holds good for the equally small Sphaeriidae.

Such limitations determine, in many cases, the lower size limit of a group of animals. Most important in this respect is probably the limitation of egg number (Rensch, 1947). Since the size of eggs cannot be indefinitely reduced for ecological and cytological reasons, the smallest animals can often contain only one mature egg in their uterus, e.g., the smallest Gastrotricha and Rotatoria, the minute marine prosobranch *Caecum glabrum*, and probably also the very small frog *Phyllobates limbatus* of Cuba. Only 1–2 eggs ripen simultaneously in very small land snails, e.g., species of *Vertigo*, *Punctum pygmaeum*, *Pyramidula rupestris*, etc. A further evolutionary decrease in size of such small animals is therefore not probable.

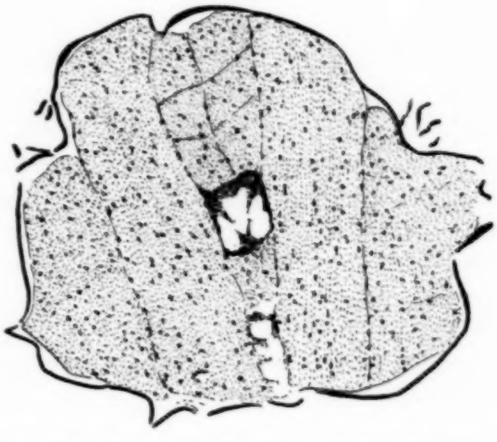

FIG. 12. Cross section through the thorax of the aphid *Phoradon persicae*. It is filled to capacity by flight muscles.

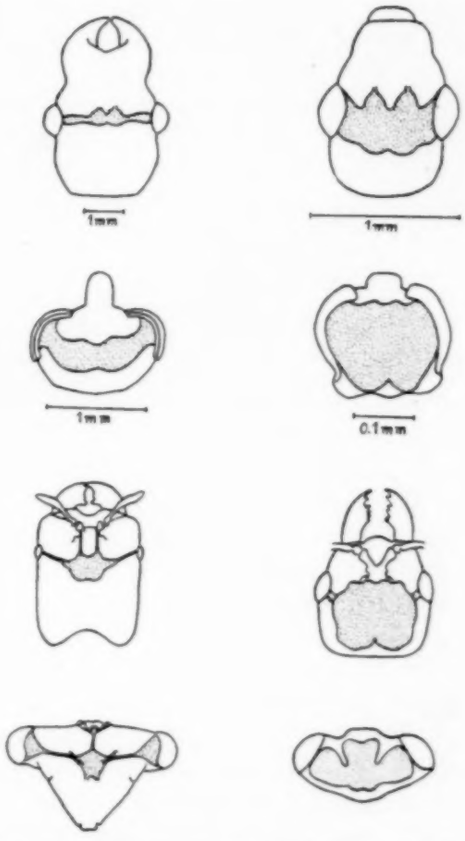

FIG. 13. Filling of the head case with brain in related species of different size. Top row, Carabidae: left, *Carabus nemoralis;* right, *Argutor diligens*. Second row, Nematocera: left, *Ctenophora atrata;* right, *Rhabdophaga heterobia* (after Goossen). Third row, Formicidae: left, *Pheidole instabilis*, soldier; right, worker (after Wheeler). Bottom row, Homoptera: left, *Cicada fraxinis* (after Berlese); right, *Phoradon persicae*.

The lower limit of body size is controlled also by a maximum filling of the body with organs. As shown in figure 2, the thorax is completely filled with flight muscles in the smallest gall-midges (Ceci-

domyidae). The same occurs in small plant lice (Aphidae) (fig. 12), etc. The ventral cord of the nervous system and also the intestine occupy relatively much space in small species, whereas there is no space left for air sacs of the tracheal system. The head capsule of very small insects is almost completely occupied by the central nervous system, as shown in figure 13 for several groups of insects. Here too an even more extreme filling up of the head capsule, i.e., a continued evolutionary decrease of body size is improbable, inasmuch as even within the brain the individual masses are often strongly pressed together like the three optic masses mentioned above. A terminal stage of evolution among very small insects is also reached in respect to the shape of the intestinal cells. As figure 7 shows, the tendency of cell shortening has resulted in the smallest species in the development of a single layer of very flat cells. Thus, the lower limit of function is reached or probably already overstepped, for the middle intestine can now perhaps work only inefficiently, that is to say, may be suited only for a special type of food like that of the aphids.

In this manner the smallest known species of each group of animals are characterized by the most complete utilization of space in the body and by the reduction of the organs to the indispensable minimum.

4. Alterations of Construction at the Lower Limit of Body Size

It is known that a more or less steady increase of body size has occurred (Cope's Rule) in the course of the evolution of many groups of animals and especially of vertebrates. Nevertheless, we may presume that a continued diminution of size offers selective advantages in the case of some already very small species because in this way still unoccupied niches of the habitat become accessible, or perhaps because the general advantages (more intensive metabolism, quicker succession of generations, etc.) are favorable. A further decrease of size has apparently taken place sometimes in lines of descent in which the existing structures had already been reduced to a minimum. In such cases a change of construction is necessary. I have shown previously (1947, fig. 46) that the pelvis of very small mammals is modified by the temporary or constant opening of the symphysis of the pubis because in these very small species the young are relatively too large or too large-headed at birth to pass through a normally-shaped pelvis. On the same occasion I demonstrated (op. cit., figs. 47–48) that the cell layers of the retina are thickened in very small birds and mammals in order to make possible a sufficient resolution of the image in spite of the small size of the eye.

Similar changes of construction or function are found also in other cases. For instance, in very small insects, where the brain has only little room in the head capsule, the optic lobes are attached at an angle (figs. 8, 13). As the number of ommatidia of very small insects is low because the size of the cells cannot be indefinitely decreased, these species have a very limited capacity for seeing the configuration of the surroundings. The eyes therefore have become unimportant and changes of instinct may take place. The smallest workers of the ant *Atta sexdens*, which only have two to three ommatidia on each side, work nearly always in the dark interior of the nest, and they do not gather building material as do the larger workers (0.9–3.3 mm. long) (Goetsch, 1940).

The above described maximum filling of the thorax with flight muscles in small insects limits the decrease of the body size, but this limit too is overcome by a change of construction. Since the muscles, if further reduced, are no longer sufficient for flight, a mechanism for floating in the air was developed by long ciliated wings which enable the insect to make use of the viscosity of the air. Such fringes on the wings are found among the smallest species of very heterogeneous orders of insects; on the fore and hind wing of Thysanoptera (some species were cap-

tured by airplanes at great heights), in the small Hymenoptera *Alaptus* (Mymaridae) and *Prestwichia* of only 0.2 mm. length (the latter floating also under water), in the smallest Zoraptera and Corrodentia, and at the hind wings of the dwarf beetles (Ptiliidae), point beetles (Clambidae), and Sphaeriidae of 0.3–1.5 mm. length, as well as on the wings of the smallest moths like *Lyonetia* (fig. 14), but in a less pronounced manner also among most of the other very small insects (e.g., among the Chrysomelidae in *Haltica*, among winged Pselaphidae,

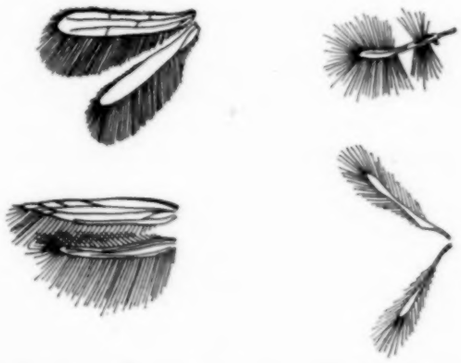

FIG. 14. Change of construction in very small insects: development of long ciliated wings. Above: left, *Aeolothrips fasciata* (Thysanoptera); right, *Oligella foveolata* (Coleoptera). Below: left, *Lyonetia* spec. (Lepidoptera); right, *Alaptus* spec. (Hymenoptera) (after Handlirsch and Sharp).

among the small Ichneumons, in the small Chalcididae, etc.).

The circulatory system of the smallest Archiannelids shows another interesting change of construction. The larger representatives of this group of worms (not distinctly separated from the Polychaeta), like *Protodrilus* (body length 1–20 mm., mostly more than 3–4 mm.), have a system of branched blood vessels like the Polychaeta. The genus *Nerilla* (1–2 mm. long) has developed a compact blood sinus, surrounding the stomach dorsally and laterally from which a vessel arises dorsally. This goes forward, bifurcates there, turns down to the ventral side, and reunites into a ventral vessel. The still smaller *Dinophilus gyrociliatus* (0.7–1.3 mm. long) has only a blood sinus around the stomach and a ventral vessel in the region of the ovarium. Finally, in *Diurodrilus* (only 0.3 mm. long) the circulatory system has entirely disappeared. It is superfluous in such a small organism since diffusion alone can supply the needs of the tissues (Remane, 1932). In the microscopic Oligochaet *Aeolosoma* a parallel development took place, closely corresponding to the *Nerilla* type.

An interesting change of function occurs in the minute marine prosobranch *Caecum glabrum* (shell 1 mm. long). It does not move like other snails with the aid of contractions of the foot muscles, for these are strongly reduced as mentioned above, but solely by the stroke of ciliae (Götze, 1938).

Such changes of construction and of function must be considered as secondary consequences of the manifold histological alterations of structure connected with evolutionary increase or decrease of body size, partly owing to allometry, partly due to the directing effect of selection.

SUMMARY

1. The analysis of the alterations of proportion, connected with changes of body size, requires not only the examination of the growth gradients in development but also of the selective influences. A large species is not merely an allometrically changed version of its small ancestor.

2. Evolutionary changes of body size often produce accompanying obligatory histological alterations of structure. An increase of the body size thus produces in several cases new structures, a phenomenon demonstrated for the flight muscles, the middle intestine, and the brain of insects.

3. The differentiation and shape of the corpora pedunculata is not only an index of the evolutionary level of the insect species in question, but it also depends on the body size. The adjacent globuli cells are much more numerous in larger species.

4. In the vertebrate forebrain the histologically recognizable regions of the cortex have different growth ratios. The evolutionary increase in size (Cope's Rule) therefore causes a strong modification of brain structure.

5. In very small species of a group of animals some organs either disappear (e.g., the penis of very small land Prosobranchia, segments of the tarsus in certain insects), or are reduced to the minimum limits.

6. The lower limit of body size within a group of winged insects is in part controlled by the maximum filling of the thorax with flight muscles and of the head capsule with brain.

7. Changes of construction and of function that compensate for structural disadvantages of the minimum size may take place near the lower limit of body size. The development of long fringes on the wings of very small insects of several orders is an example of this phenomenon.

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GEOGRAPHY OF HUMAN BLOOD GROUPS (A, B, O SYSTEM)

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The distribution of the alleles of the AB blood group is of great importance in physical anthropology since it is the only human racial character whose genetics is fully clear,[1] and which has been studied intensively and with exact methods. As far as is known, the gene is not linked with any other gene, nor do the blood group genes control any other physiological characters. This means that so far as is known they have no selective significance. The mutation frequencies are evidently very low. This is shown, in the huge body of genetical material collected all over the world, by the great similarity in the frequencies of the alleles between related ethnic groups which have been separated from each other for centuries and have not mingled with other groups for centuries. Thus, unmixed gypsies have nearly the same ratios as the present natives of their ancestral home in India; German colonists in south Hungary have the same frequencies as do the present population on the middle Rhine area, although the colonists left the Rhineland hundreds of years ago (Hirszfeld, 1928).

The frequencies of blood alleles, "the serological pattern," are thus a first-rate indication of origin. However, the rule of the variability of the allele ratios within a human group is subjected to the law of chance. Hence the above-mentioned fact of the invariability of the pattern is true only of large-sized populations. Within areas of limited population, e.g., a rural parish, new relations between the alleles may develop, especially after wars, plagues, etc., when the population has been further reduced.

THE DISTRIBUTION OF THE DIFFERENT ALLELES

The allele p is distributed in variable frequencies all over the world (map 1) with the exception of America, where it is fairly rare. It is also sparse in east Africa and in the interior of Arabia. Very high frequencies are found in the following four regions: (1) The whole of Europe with a great part of the Near East excepting Arabia, but including Egypt and the northern half of the Somali Peninsula. (2) The Australian continent but not New Guinea. (3) The outer (eastern) part of Polynesia. (4) Japan, and also a great part of China. Further, p is common in Tibet and most of the Himalayan countries, and also among many primitive tribes. Besides the above-mentioned Australian aborigines, it is common among Bushmen in South Africa, Congo pygmies, negritos in the Philippine Islands, and some "hill tribes" of south India; it is also frequent among many Eskimos and some Indians of the northwestern part of the United States.

The allele q (maps 2 and 3) has its greatest frequency in central Asia and in northern and central India—in both regions, curiously enough, with about the same mean percentage, i.e., 27 per cent; but it has lower ratios in most of the intervening Himalayan countries; q is also very frequent in Egypt and among the Congo pygmies. In relation to p, q is rather frequent in the whole of central and western Africa, but sparse in the south and east. In the latter regions, it is more

[1] In the following study we use only the allele frequencies (p, q, r), not the frequencies of phenotypes (A, B, O, AB).

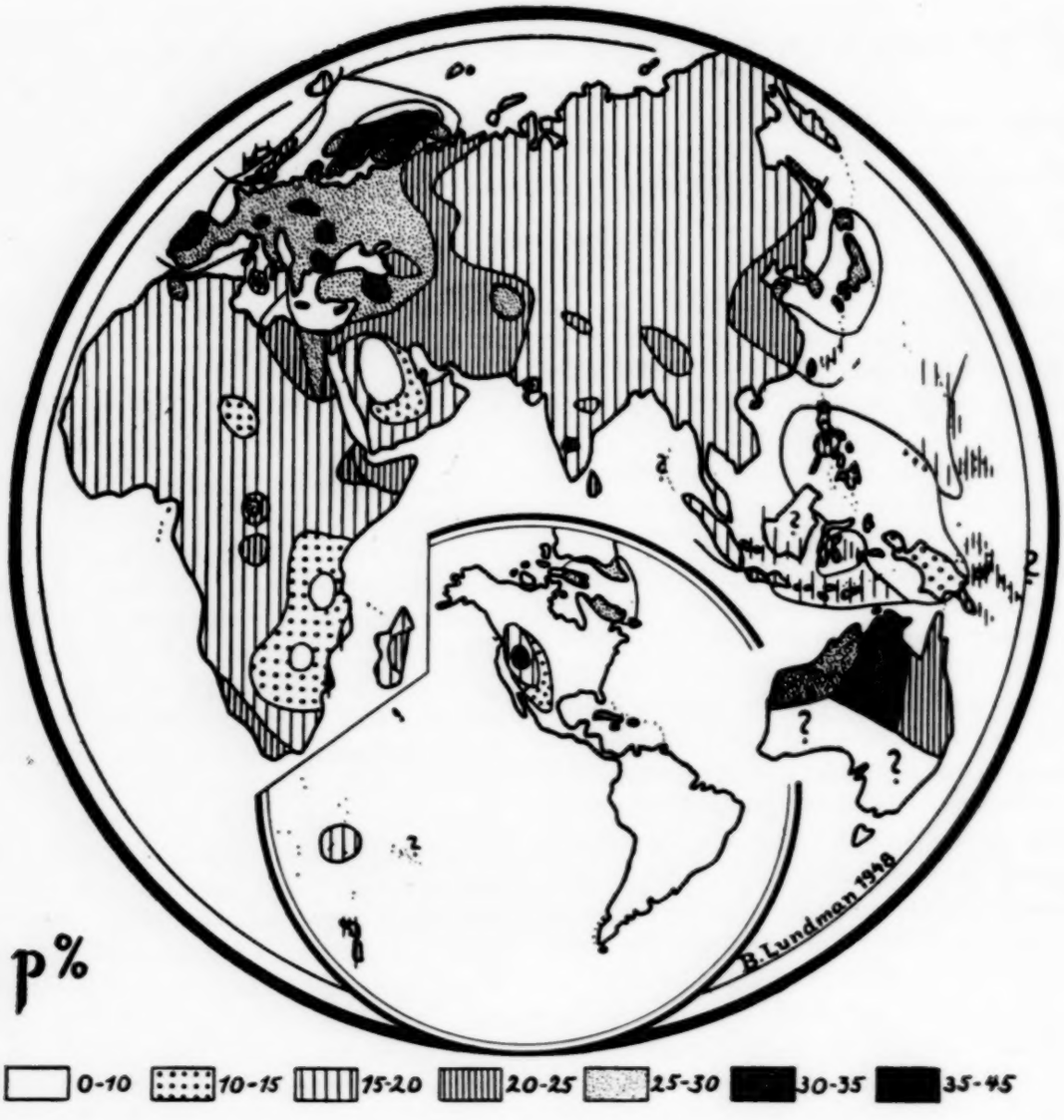

FIG. 1. Map of frequencies of blood allele *p*.

abundant only among the Hottentots and Somalis. In America *q* is extremely rare among the indigenous races. Some tribes in the southern part of South America may have a little more of that allele, but the material from there is extremely small and possibly not always reliable. *q* is also found in very low percentages on the Australian continent, in great parts (especially the outer ones) of Polynesia and in central Arabia. In Europe *q* is most frequent in the east among the Finns, the east and west Slavs, and in the northeastern parts of the Balkan Peninsula. In the west of Europe it is rather rare. Northern and eastern Germany (of 1919–1938), east of the Elbe, has an intermediate position, yet nearer to the west than to the east. Curiously enough, *q* is again fairly common in westernmost Europe in many Celtic districts of Great Britain.

The allele *r* (map 4) is the most common of all the alleles throughout the world although it is possible that its frequency is no greater than that of *p* among some hill tribes in South Deccan and among the Blackfeet and the Blood Indians in the northwestern part of the United States. The frequency of *r* is not only greater

than that of either of the other alleles, but in most countries it is greater than that of both of the other alleles combined. Only relative dominance (and then at frequencies only very little below 50 per cent) is known, in addition to the mentioned small tribes of India and the United States, in parts of Egypt, among some Mongolian tribes in central Asia, and among some of the Congo pygmies. In nearly all Indians *r* prevails almost to the exclusion of the other alleles (90–100 per cent) and the small amount of the two other alleles is usually but not always (cf. the above-named U. S. A. Indians) the result of post-Columbian minglings. Still, it cannot be assumed that *p* and *q* originated in the Old World after the departure of the Indians to America, for these alleles are found even among the apes.

Geographic Synthesis

In spite of all irregularities, the world may be divided into a rather restricted number of tolerably homogenous "serological provinces" (map 5). Between them we often must insert transitional belts and here and there isolated aberrant islets. Furthermore, data from the Tibetan-Himalayan region are nearly un-

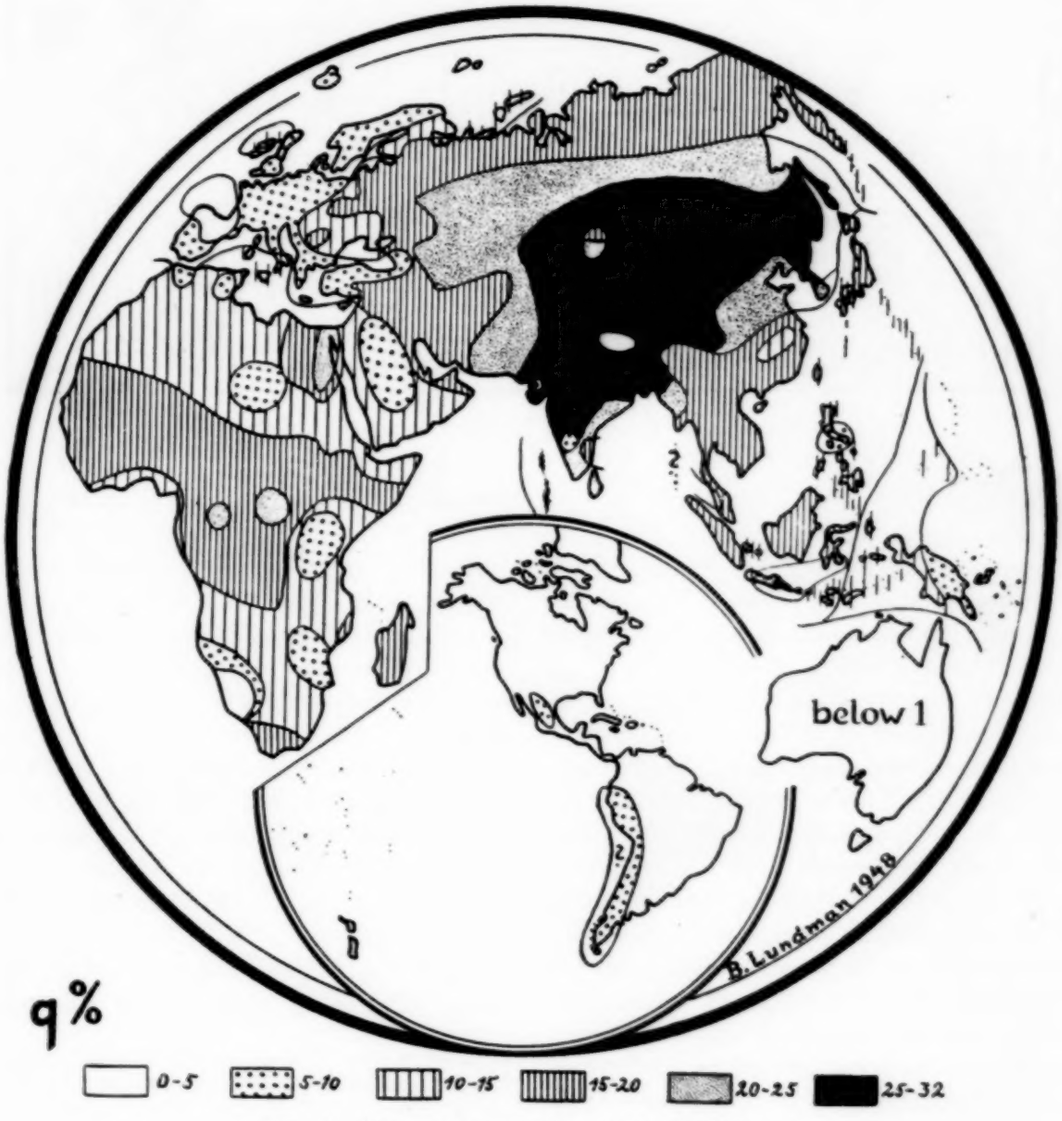

Fig. 2. Map of frequencies of blood allele *q*.

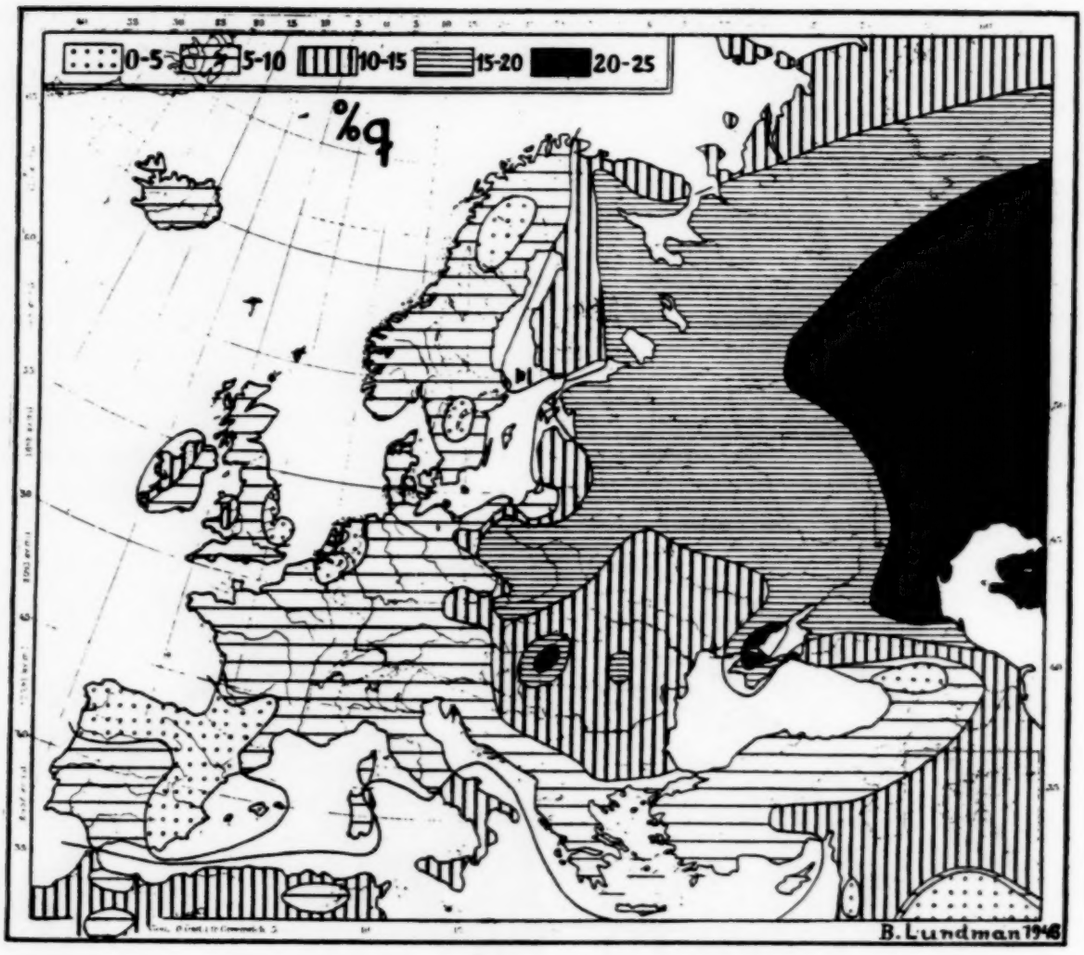

FIG. 3. Map of frequencies in Europe of blood allele *q*.

known and that area is marked with a question mark on the map. Western Europe and the Near East (except Arabia) form a special province (A on the map) which is especially rich in *p* and poor in *q*. Central Asia (B 1), rich in *q*, forms another serological province. The above mentioned little known Himalayan tribes indicate different, more "European" conditions, but north and central India (B 2 on the map) have again about the same allele frequencies as B 1. Region C on the map fills out the arid regions which border the Indian Ocean from Arabia through eastern to South Africa, with interruptions for some coastal belts (Somalia) and the shores of the great river Zambezi. In C *r* is abundant while *p* is rare, and *q* even rarer. The central African forests and Upper Guinea (D) have a greater frequency of *q* and to some extent also of *p*.

Between these main regions in the western half of the Old World lie several broad transitional zones [2] and also small aberrant districts, especially among British Celts, Egyptians, Congo pygmies, and Bushmen. Curiously enough, the ratio *p*:*q* is the same in nearly all Africa except among Bushmen, the steppe tribes in Tanganyika, and in the whole northwestern part, even though the *r* frequencies of the Egyptians and Kaffirs are very different.

Such serological regions are a little more difficult to construct in the whole

[2] The eastern European belt between A and B has independence, having a *p* rate nearer A and an *r* rate nearer B, but being rather intermediate in the *q* rate.

eastern half of the Old World and in Oceania. Partly, as in Indo-China and parts of Polynesia, the material is scanty; partly (especially in Java) great contrasts are encountered in neighboring populations. Yet, we find the Japanese region (E) with much p and q, a rather indistinctly marked region in central and south China, Indo-China and Indonesia (F), a Melanesian region with much more r (G), and a central Australian region (H) that is extremely rich in p. The native races of America constitute a great region (J) with the exception of the aberrant Eskimos and the above-mentioned strange tribes in the northwestern part of the United States. This completes the delimitation of all the serological regions.

Discussion

As has been implied above, the correlation between racial relationship and serological similarity is not very close. Central Mongols and Hindus, physically so utterly unlike, exhibit practically the same serological pattern. The Egyptians and the central Arabians differ extremely in this respect from each other, but are racially rather closely related to Mediterranean peoples.

Fig. 4. Map of frequencies of blood allele r.

FIG. 5. Map of serological regions.

Single letters (also B 1 and B 2) see text. Double letters = mixed regions. Small aberrant districts are marked black on the map.

Evidently the explanation is that the parentage here goes back to times when the nowadays-serologically differing, but undoubtedly racially related, groups were so small that chance (in combination with time) was able to displace the ratios of the alleles to a great extent. More difficult to explain is the astonishingly great similarity in serological pattern between the central Mongols and the Hindus, but here mere chance is a probable explanation. Strange is also the serological likeness between the Scandinavians and most of the Greenland Eskimos. It is too great and the races are too distantly related to permit explaining the whole matter as a consequence of the slight amount of comparatively recent intermarriage between the Eskimos and Danes (and possibly Norsemen in the Middle Ages). The very close serological resemblances between Scandinavians and Scandinavian Lapps, and between Japanese and Ainus, are similar situations. It is not clear how one should explain the origin of a few Indian tribes extremely rich in p in the midst of the large American Indian population almost devoid of p. Should one apply the elimination theory here of the r allele in the very small origi-

nal group, or postulate mutations in old times? The first seems more probable to the present author. On the whole, the elimination theory explains many irregularities of the blood alleles. It makes the scientist less inclined to construct great world-embracing wanderings of peoples in prehistoric times, only on the basis of modern serological values. But, it cannot be denied that the theory of the relative intactness of the Columbian races of America from relatively late, but pre-Columbian invasions from the Old World is strongly supported by the A–B–O serology.

The distribution of the blood alleles is of considerable value in helping to determine the parentage of those ethnical groups which, after their comparatively recent separation, have not been subject to the modifying effects of small population size; also in cases of mass emigration in historical times. An analysis of the blood alleles of mixed population groups sometimes permits the calculation of the numerical contribution of the two components of the mixture, but it is outside the scope of this short paper to substantiate this statement with concrete examples.

On the other hand, the significance of the serological pattern is small or nil as an indicator of ancient racial connections or for the identification of small family groups in our time. In spite of these shortcomings the maps of the distribution of the blood alleles are of great general biological interest as genetic maps based on extensive material derived from all parts of the world.

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Explanation of the Maps

These are the only fairly detailed and accurate maps of the world distribution of the blood alleles that are available. They are based on published material known to the author. Unpublished series have hardly been used. Almost all of the material is found in Boyd's works and, in addition, in Gates. [The latest data from Madagascar are not accessible to the author.] For Sweden I arrived at the following values: $p = 30.9$ (± 0.20), $q = 7.6$ (± 0.15) and $r = 61.5$ (± 0.25), by pooling the hitherto published Swedish results (about 34,000 Swedes in Sweden who were blood givers in the Army [not serologically selected]). Statistics for populations that have emigrated to their modern homesteads in post-Columbian times are not included in the maps. Naturally it was necessary to make many generalizations in drawing up the maps on such a small scale.

Table 1. *Approximate values typical for focal areas of the respective regions*

Region	Per cent		
	p	*q*	*r*
A	30	7	63
B (= B 1 and B 2)	18	27	55
C	12	10	78
D	16	16	68
E	28	17	55
F	15	18	67
G	14	12	74
H	40	0	60
J	7	2	90+
C. African Pygmies	25	21	54
Egyptians	27	22	51
E. Java	13	27	60
W. Java	22	19	59
Korea	25	22	53

EVOLUTION IN THE FAMILY DICRURIDAE (BIRDS)

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I. INTRODUCTION

The knowledge that neither genetics nor systematics nor paleontology alone can solve the problems of evolution has become commonplace. But with all their limitations, each of these disciplines has its special niche in the field of evolutionary research. As far as systematics is concerned, its strength lies in the abundance of material it can supply on intraspecific variation, on the origin of discontinuities, and on the ecological relationship of closely allied species and of intraspecific populations.

Evolutionary patterns depend, as has become increasingly clear, to a great extent on the ecological conditions to which an organism or group of organisms is exposed. In order to arrive at valid generalizations, it therefore becomes necessary to study the evolution of as many ecologically different kinds of organisms as is possible. Furthermore, it becomes desirable to study them quantitatively. Finally, it is advisable to study entire groups in order to avoid the objection of the selection of biased examples.

The present analysis is based on a detailed taxonomic revision of the bird family Dicruridae or drongos by the junior author. This family has the advantage of small size (twenty species only) and of being well known taxonomically. It is unlikely that any new species remains to be discovered and even the description of subspecies has nearly reached an end. All but six of the species were described before 1840. The last six species (all from islands or mountains) were described in 1866, 1867, 1874, 1887, 1893, and 1919. The revision of the family (Vaurie, 1948) is based on an examination of about 3500 specimens of each of which four to seven measurements were taken. Adequate samples of all but three of the one hundred recognized subspecies were examined.

The Family Dicruridae

This family consists of twenty species of medium-sized passerine birds. The coloration is in most species black with a pronounced greenish, bluish or purple gloss on certain parts of the plumage. Bill, legs, and feet are always black. The iris is usually red in adults and always brown in immatures. Both sexes are identical in coloration in all the species, but females average consistently smaller. The plumage is molted once a year. Immatures differ from adults in a number of minor characters, and may not attain the adult plumage in some species until the third year.

It is characteristic of the present status of bird taxonomy that the relationship of species and subspecies within the family can be worked out down to the most elaborate details, while it is as yet impossible to give a clearcut diagnosis for the family as a whole, or to state its nearest relatives. The Dicruridae are usually placed near the Corvidae (crow family), apparently for no better reason than that they are black. Other authors have placed them near the shrikes (Laniidae) or the flycatchers (Muscicapidae) on the basis of certain adaptive similarities in bill structure. Relationship with the Campephagidae (cuckoo-shrikes) and Paradisaeidae (birds-of-paradise) has also been suggested. Since the family seems devoid of any diagnostic character, it appears probable that it may have to be reduced to the rank of a subfamily, but it is not even known as yet of what family.

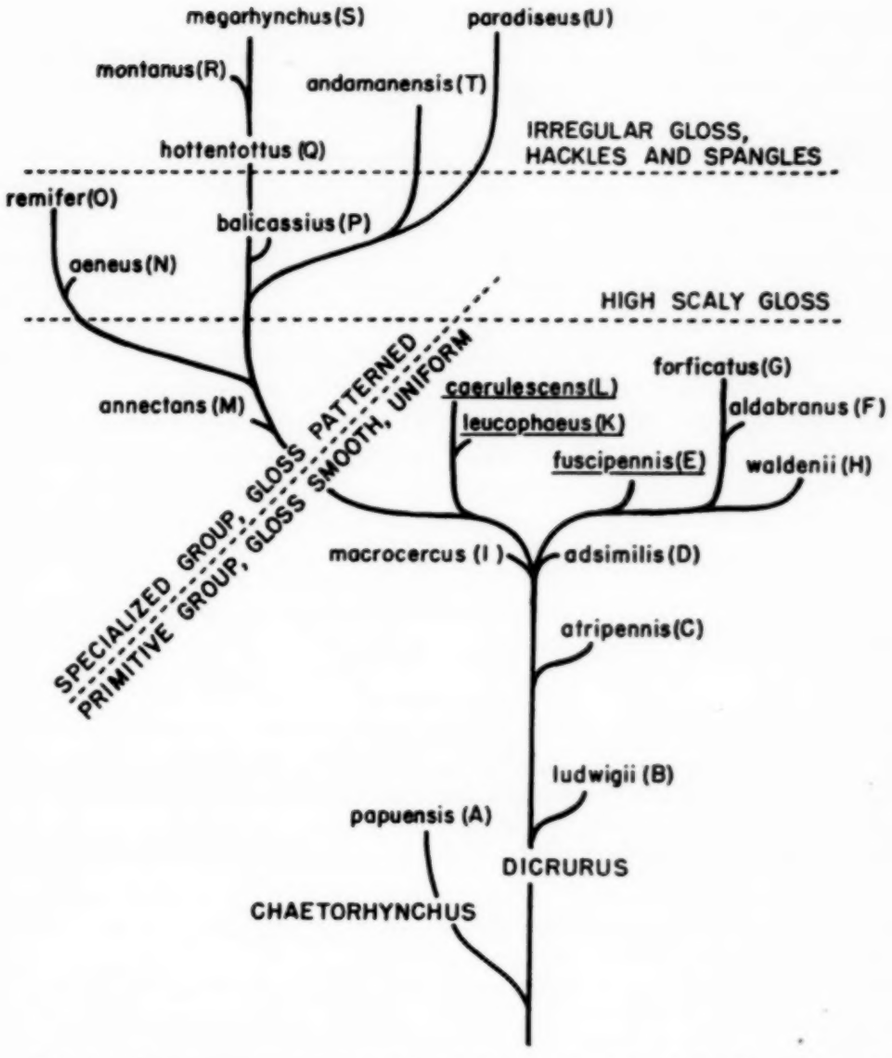

FIG. 1. Diagrammatic presentation of the relationship of the 20 species of drongos. Trends in pigmentation indicated by groupings separated by broken lines. Underlined species show tendency for loss of pigmentation.

Although the correct placing of the family in relation to the other families of song birds is so far impossible, there is no difficulty in recognizing any member of this family as a drongo. The Dicruridae are a compact and very characteristic group of species.

Primitive and Specialized Species

When lacking fossil evidence, students of recent species are not in the position to establish reliable phylogenetic "trees." They would not be able to reconstruct even diagrammatic phylogenies, if it were not for one curious fact. There are unspecialized, "primitive" species and genera in most families, together with others that show various degrees of specialization. It appears as if a number of species had "stopped" at various points along the road away from the ancestral position. No living species can be the ancestor of any other living species. However, by eliminating certain specialized features, it is possible to reconstruct the appearance of the putative ancestor of a species, and then it is often found that this reconstructed ancestor resembles very closely an existing species. The attached diagrammatic family tree of the drongos was recon-

structed with the help of such considerations (fig. 1). It is not a representation of the actual phylogeny in time or space.

Chaetorhynchus papuensis is placed at the bottom of the phylogeny, since it is the only drongo that still has twelve tail feathers, like most passerine birds. All other drongos have lost one pair and possess only ten tail feathers.

The other nineteen species divide rather easily into two sections, a primitive one (a) and a more specialized one (b).

(a) The *adsimilis* section (Species B–L). Plumage with moderate gloss. No hackles or spangles. Crest absent (except in *forficatus*). Wing often brownish. Black of body plumage not always intense, and modified into gray or brown in a number of species. Tail forked, deeply in the large, slightly in the small species. No special modifications of outermost tail feathers.

All the African species belong to this group, as well as a few closely related Asiatic species (*macrocercus, leucophaeus,* and *caerulescens*). Although the group as a whole is primitive, it contains several species that have become specialized in various directions without entirely losing the group characteristics.

TABLE 1. *Check-list of the species of drongos*

Genus *Chaetorhynchus*

A. *Chaetorhynchus papuensis*. Mountains of New Guinea.

Genus *Dicrurus*

Section 1

B. *ludwigii* (2)*. Ethiopian Region from Senegal and southern Sudan southward.
C. *atripennis*. Restricted to the Upper and Lower Guinea rain forest.
D–I. Superspecies *adsimilis*
  D. *adsimilis* (5). The whole of the Ethiopian Region, including Principe Island.
  E. *fuscipennis*. Grand Comoro Island.
  F. *aldabranus*. Aldabra Island.
  G. *forficatus* (2). Madagascar and Anjouan.
  H. *waldenii*. Mayotte Island.
  I. *macrocercus* (7). Southern Asia from eastern Afghanistan along the southern Himalayas, Ceylon, Indo-Chinese countries eastward through China as far north as the Amur River, as far south as Tenasserim, Java, Bali, Hainan, Formosa. [Migratory in parts.]
K. *leucophaeus* (15). Southern Asia from eastern Afghanistan along the southern Himalayas through India, Indo-Chinese countries, to northern China into Manchuria, Hainan, Malaya, the whole of the Sunda Shelf, plus the western Sumatran Islands and Lombok. [Migratory in parts.]
L. *caerulescens* (3). India from southern Himalayas into Ceylon.

Section 2

M. *annectans*. Himalayas from Nepal eastward to Burma and Siam (migratory, winters in Borneo, etc.).
N. *aeneus* (3). India, and Indo-Malaya (except Java and Bali), and Formosa.
O. *remifer* (4). Himalayas from Nepal eastward to southern China, Indo-Malaya except Bali, Borneo, and neighboring islands.
P. *balicassius* (3). Northern and central Philippines.
Q–S. Superspecies *hottentottus*
  Q. *hottentottus* (32). Southern Asia from Punjab along the southern Himalayas through India, Indo-Chinese countries, to northern China, the whole of Indo-Malaya, southern Philippines, the whole of Indonesia and of the Australo-Papuan Region to the eastern Solomons and southeastern Australia. [Migratory in parts.]
  R. *montanus*. Mountains of Celebes.
  S. *megarhynchus*. New Ireland.
T. *andamanensis* (2). Andamans (Great Coco and Table Islands).
U. *paradiseus* (14). India from Kashmir along the southern Himalayas to western Yunnan, southward to Ceylon and through Indo-Malaya, Hainan, and the whole of the Sunda Shelf except Bali and Palawan. Also, the Andamans, Nicobars, Simalur, Lasia, and Babi Islands.

*Figures in parenthesis refer to number of subspecies.

(b) The higher drongos (Species M–U). Plumage either with high metallic gloss (*aeneus-remifer*) or with distinct glossy "spangles," "hackles," or both. Wings very black and glossy. Outermost tail feathers often modified in the more long-tailed forms. Occasionally crested. The species *annectans* forms a perfect link between this group and the *adsimilis* section.

The seven species and superspecies of this group are restricted to the Oriental Region, except one which extends far into the Australo-Papuan Region.

A concise check-list of these twenty species and their principal distribution is given in table I.

The Genera of Dicruridae

Not less than twenty-two generic names have been proposed in the course of time for the thirteen species and superspecies of drongos. Sharpe in his Handlist of birds (1909) admits twelve genera as valid while an additional genus has since been described. This amounts virtually to mononomialism. Actually matters are even worse, since five primitive species were included in a single genus, while various members of the superspecies *hottentottus* were classified in four distinct genera, different subspecies of *D. paradiseus* in two genera.

Such classification completely obscures true relationship. It is based on the overrating of a few specialized ornaments like crests or modifications of the outermost tail-feathers. These may originate repeatedly in independent lines as will be shown in a later section. Furthermore, all the various characters that were used in the past for generic separation of species of drongos may vary geographically. This is true for the intensity of gloss, shape of the tail, depth of the fork, shape of the bill, and presence or absence of a crest.

The only consistent solution is to unite twelve species and superspecies in the genus *Dicrurus* and to admit a separate genus (*Chaetorhynchus*) only for the aberrant New Guinea species *papuensis* which still retains the primitive number of twelve tail feathers (Vaurie, 1948).

II. Taxonomic Characters and Their Evolution

The question of the origin of new taxonomic characters figures prominently in all discussions of the origin of the higher categories. The problem remains essentially the same whether polytypic species are included among these higher categories, as by Kinsey (1936), or whether they are restricted to orders, classes, and phyla, as by the paleontologist (Jepsen, 1943). In either case there is the question how the characters arise, which distinguish one taxonomic unit from another, and under what circumstances they become modified or lost during evolutionary history. The completeness of knowledge of the living Dicruridae makes them exceptional material for an analysis of the evolutionary fate of the principal characters known to vary within the family. An attempt can be made to establish the various evolutionary trends within the family, to investigate the geographical variation of these characters within the various species, and to correlate this variation with features of the environment (climate, geographical discontinuities, etc.).

Morphological characters that contribute to the differences between species of drongos are general size, length of the tail, depth of tail furcation, amount of gloss, development of spangles and hackles, presence or absence of a crest, modifications of the outermost tail feathers, etc. In addition there are differences in habits and ecology. The extent to which these characters show evolutionary trends between and within species, will be investigated in the subsequent sections.

Evolutionary trends. Paleontologists have described in much detail many instances of remarkable evolutionary changes in a single organ or structure, such as the horns of the titanotheres or the teeth of the horses. Similar phylogenetic studies

are impossible in birds in view of the scantiness of fossil remains. However, comparable studies can be undertaken with living species, since differences between contemporary populations often form parallels to phylogenetic series. Here also unspecialized, "primitive" species can be distinguished as well as all sorts of stages of greater and greater specialization in various directions. By tracing the changes

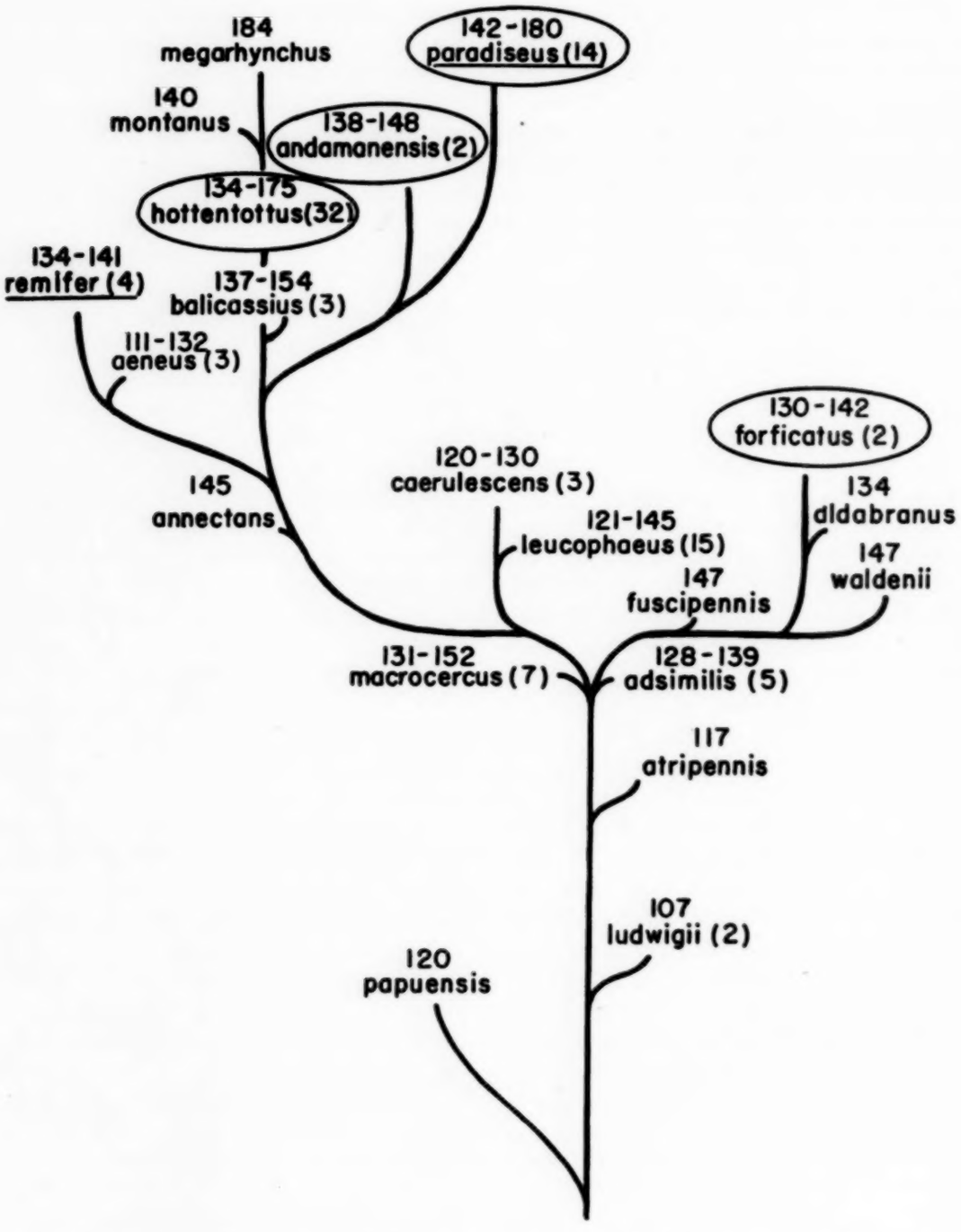

FIG. 2. Size variation and parallelism in drongos. Figures in parentheses after species name indicate number of recognized subspecies. Figure above species name indicates mean wing length of adult males, in polytypic species of the smallest and largest subspecies. Crested species are encircled; species with tail rackets are underlined.

of a number of selected characters through the entire family of the drongos the potentialities of this family can be studied and it can be shown in what manner these characters have become realized in the various branches of the family.

Size

Since weights are available only for a few specimens in three or four of the species, size is best expressed in terms of "wing-length," which in birds is fairly closely correlated with general body size.

The smallest species of the family is *D. ludwigii* with a mean wing-length in adult males of 107 mm., the largest is the giant *D. megarhynchus* (184 mm.). In fourteen species the mean of wing length of adult males varies within the narrow range of 130 to 150 mm. The three smallest species, *D. ludwigii* (107), *D. atripennis* (117), and *Ch. papuensis* (120), are also the three species which for independent morphological reasons have been considered the three most primitive species of the genus. On the other hand, the three largest forms, *D. hottentottus megalornis* (175), *D. paradiseus grandis* (180), and *D. megarhynchus* (184), are members of the morphologically most specialized group (fig. 2). This confirms two principles well known in mammalian evolution. First, that in many evolutionary lines there is an increase in size, and second that owing to allometric growth the largest forms tend to have the most pronounced development of specialized structures.

Pigmentation and Gloss

The amount and the distribution of gloss on the black plumage shows definite evolutionary trends among the Dicruridae. The primitive species are black with a more or less even, subdued, greenish, bluish or purple gloss. Three trends away from this primitive condition can be observed, (a) toward a reduction of the black coloration together with loss of gloss, (b) toward a uniform intensification of gloss, and (c) toward a modification of the feathers into spangles, hackles, and velvety feathers. Figure 1 shows that each of these trends is realized in a different group of closely related species.

Gloss is lost in those species or subspecies that have also lost the intense black pigmentation. This is characteristic for some species of the superspecies *D. adsimilis*, for *D. caerulescens*, and for most forms of *D. leucophaeus*. It might appear at first that the grayish coloration of these forms is more primitive than the black of all other species, but there is much evidence against such a point of view. The three otherwise most primitive species of the family are glossy and black. In superspecies *adsimilis* loss of pigment and of gloss is found only in a few aberrant island species, where it is clearly a secondary phenomenon. In *D. leucophaeus* there is strong geographical variation in this character (fig. 7). The most pronounced loss of pigment occurs in the obviously "young" form of northern China. These facts combined support the contention that reduction of pigment and absence of gloss are a secondary development in this family.

A high metallic gloss has evolved in *aeneus* and *remifer*, and this gloss tends to be restricted to certain parts of the feather and to certain areas of the body. This is also true of *balicassius* in which there is a tendency toward the formation of spangles. Among the more primitive species fairly high gloss occurs in *atripennis*, but there is no trace of a scaly modification of the feathers.

The higher species (*annectans*, etc.) are characterized by various modifications of the feathers. Their shape tends to become narrower and more pointed, culminating in the long hackles found in *hottentottus* and *paradiseus*. Simultaneously, there is a localization of gloss either along the margin or in the center of the feather. Finally, in *hottentottus* gloss is replaced on the back by a velvety feather structure.

Proportions

The species and subspecies of Dicruridae are very plastic in the proportions of their appendages. This is particularly true for the tail, less so for the bill. A forked tail of about 90–100 per cent of the length of the wing is considered typical of the family. Lengthening of the tail and deepening of the fork are the chief trends away from this primitive condition.

Relative length of the tail. General body size and relative length of the tail are loosely correlated in drongos. The large forms tend to have relatively long tails, the small forms short ones. The three smallest species (*papuensis, ludwigii,* and *atripennis*) have a rather short tail, the outermost (longest) tail feather measuring about 80–95 per cent of the length of the wing. However, some of the medium-sized species (*annectans, balicassius*) have equally short tails (77–87 per cent), while some of the smaller races of the *hottentottus* have even shorter tails: *samarensis* (66–71 per cent), *sumatranus* (69.5–71.5 per cent), *borneensis* (77–80 per cent), and *brevirostris* (79–83 per cent). The longest tails are found in a few aberrant island forms: *waldenii* [Mayotte Island] (140 per cent), *menagei* [Tablas, Philippines] (129 per cent), and *megarhynchus* [New Ireland] (202–213 per cent). *D. macrocercus* has consistently a long tail in all subspecies (97.65, 99.5, 105, 110, 111, 118.75, and 124 per cent average in seven subspecies.) The two species with racket tails (*paradiseus* and *remifer*) are not included in this tabulation, since the absence of a web on part of the outermost tail feather is correlated with an extreme elongation of these feathers, reaching 276 in *D. paradiseus grandis* and 446 in *D. remifer lefoli.*

Depth of fork. The character most frequently cited as characteristic for the drongo family is the forked tail. Actually, the most primitive species, *Chaetorhynchus papuensis,* has a rounded tail in which the outermost tail feathers are shorter than the central ones. The depth of the fork is very shallow in some of the other species and subspecies. One generalization, however, is conspicuously evident: the fork is much deeper in the species and subspecies with a long tail than in those with a short one. It is only 1.1 per cent of the length of the longest tail feather in *samarensis,* 6.6 per cent in *sumatranus,* 7.4 per cent in *ludwigii,* while the depth of the fork amounts to 38 per cent in *menagei,* 43.7 per cent in *waldenii,* and 60 per cent in *megarhynchus.* The fact that the fork of short-tailed forms is shallow and of long-tailed forms deep, in-

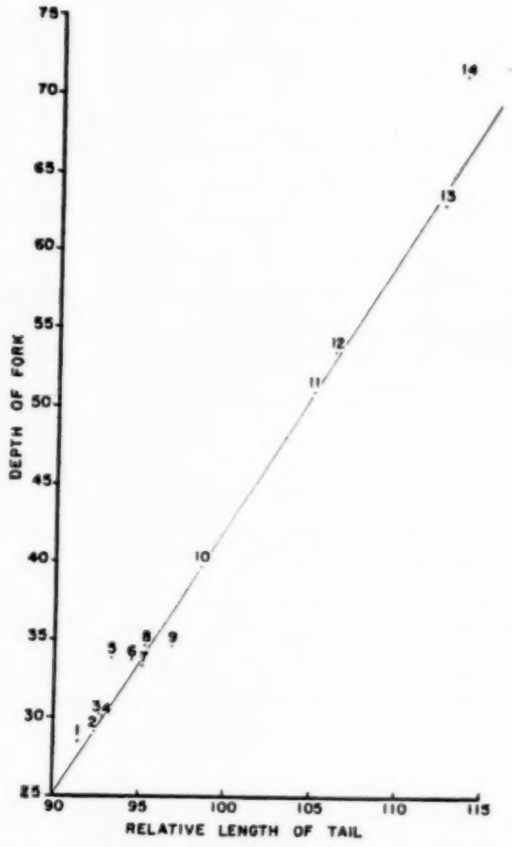

FIG. 3. Increase in the depth of the tail fork (in mm.) correlated with increase in relative length of tail (in per cent of wing length) in *D. leucophaeus.* Each point indicates the mean for the available sample of adult males of the following subspecies: 1 = *batakensis,* 2 = *leucogenis,* 3 = *phaedrus,* 4 = *stigmatops,* 5 = *siberu,* 6 = *periophthalmicus,* 7 = *salangensis,* 8 = *bondi,* 9 = *leucophaeus,* 10 = *innexus,* 11 = *mouhoti,* 12 = *hopwoodi,* 13 = *longicaudatus,* 14 = *beavani.* See also figure 7.

dicates that the evolutionary growth of the tail is allometric. The outer tail feathers increase their length much more than the central ones. Furthermore, this growth is not irregular, since a scatter diagram of the depth of fork in various species or subspecies plotted against the relative length of the outermost tail feathers (in per cent of wing length) results in a series of points that are situated on a rather narrow band as, for example, for all the races of *leucophaeus* except *beavani* (fig. 3).

The formula of the linear curve shown in figure 3 can be expressed as $x = (y\text{-}a)b$. In this formula x = the depth of the fork; y = the tail index; a = a constant which expresses the tail-index at which the depth of the fork becomes zero, and b = a constant which expresses the rate of increase of the depth of the fork. Calculation reveals that in the curve of figure 3 the numerical values of the constants are as follows: $a = 73.5$, $b = 1.58$. This means that the depth of fork would drop to zero if the tail became as short as 73.5 per cent of the wing length, and that the depth of the fork increases 1.58 times as fast as the tail index. There is more scattering in a similar graph drawn for *D. hottentottus*. In particular, the tails that are the relatively shortest and longest lie outside the graph. With short tails there develops a tendency for the depth of the fork to decrease more slowly, and with long tails to increase more quickly than in the midpart of the curve. The tail of *D. megarhynchus*, for example, is more deeply forked than it should be on the basis of the *b* value for the *D. hottentottus* group. Other strong deviations from this regression line are found in the subspecies *samarensis*, *sumatranus*, *longirostris*, and *sumbae*.

The conclusion that the form of the tail in the drongos is a function of its size is of evolutionary importance since it indicates that the highly aberrant appearing tails of *menagei* and *megarhynchus* are not evolutionary novelties, but merely extremes of a regular, continuous trend.

Size of Bill

The relative length of the bill appears to be a very irregular character in this family. It may be large or small in species of any size. This irregularity is, however, in part due to the interaction of several independent trends: small species on the average have relatively longer bills than large-sized species. Forest species have larger bills than savanna species. The relatively and absolutely longest bills are found in a few peripheral and very isolated island forms: *waldenii* (Mayotte Island), *hottentottus longirostris* (San Cristobal), *hottentottus megalornis* (Kei), and *D. megarhynchus* (New Ireland). The relative length of the bill is 30–50 per cent greater in these extreme forms than in their nearest continental relatives.

Special Structures

While the primitive species of drongos are very nondescript birds, except for the forked tail, a number of specialized structures appear among the "higher" species. They consist of modifications of the outermost tail feathers and of the feathers of the forehead.

Curled tail feathers. A tendency toward curling of the outermost pair of tail feathers is characteristic for *D. hottentottus*. This curling may reach the point where the tip of the feather not only turns completely upward and outward, but continues to twist into a tight corkscrew. Such a climax is reached in *D. megarhynchus* on one hand and in the continental races of *hottentottus* on the other (fig. 5). A similar tendency toward curling of the outermost tail feather is found also in the closely related *D. paradiseus*, but nowhere else in the genus.

Tail rackets. In two species of drongos the outermost tail feather is modified in a peculiar way. Part of the shaft is denuded, but the tip is fully webbed, forming a racket or spatula. Such tail rackets have evolved independently in two only distantly related species, *D. remifer* and *D. paradiseus* (fig. 2). The independence

of evolution of the two types of rackets is confirmed by the fact that they are quite different in construction. In *D. remifer* the racket is webbed on both sides of the shaft, in *D. paradiseus* only on the inner side (although through the twisting of the shaft it appears as if the webbed half of the feather was the outer half!).

In these two species of drongos racket feathers are absent either in the immatures (*D. remifer*) or in some or all individuals of certain geographic races (*D. paradiseus*). However, they are equally developed in both sexes, as they are in the motmots. In those hummingbirds (*Loddigesia, Discosura, Ocreatus*) in which similar racket tails are found, they are sex limited structures of the males. This is also true in the birds-of-paradise, where the flagbirds (*Parotia*) have three racket-bearing feathers on each side of the neck. True racket tails occur in no group of songbirds other than the drongos. Some even more bizarre modifications of tail feathers are found among birds-of-paradise (*Cicinnurus*).

Crest. There is a trend in the drongo family toward a modification of the frontal feathers. They are very dense and slightly lengthened in several species, including the primitive *Chaetorhynchus papuensis*. However, twice in the drongo family these frontal feathers have developed into a complete crest. Once in the Madagascar species *forficatus* and independently a second time in the group of the three closely related species *hottentottus, andamanensis,* and *paradiseus*.

Evolutionary Potentialities

There has been some confusion in the literature on evolution on the meaning of "randomness" of mutations. This term has been interpreted as meaning that a mutation might occur on any locus with equal probability. This is known not to be the case. Some loci are apparently more mutable than others. Random mutation means (a) that it is not predictable which locus will mutate next, and (b) that there is no predictable correlation between a given set of environmental conditions and the occurrence of certain mutations.

That some loci are apparently more mutable than others is indirectly confirmed by the occurrence of certain evolutionary trends (others appear to be strictly adaptive). Such trends, as they occur in the drongo family, have been described in the preceding section. Excessively long and deeply forked tails, tail rackets, and frontal crests are some of the characters that were acquired in this family repeatedly by unrelated species. However, no drongo has developed wattles or parietal crests as found among other families of songbirds. The pigmental potentialities of the family are exhausted with blacks, grays, and white, and the colors are always solid. Spotting of the plumage does not occur (except for the rictal spots of *macrocercus* and the facial mask of *leucophaeus*). Opposed to this absence of characters that are otherwise widespread among songbirds is, as mentioned, the fact that the characters that do occur among the drongos seem to have arisen independently in various branches of the family (fig. 2). This suggests that throughout the family there is a genetic predisposition toward a lengthening of the tail, toward a modification of the outermost tail feather, and toward the development of a frontal crest, a disposition that is materialized in a certain number of species. Parallelism in evolution must be accounted for by such basic similarity of the germ plasm.

Correlated and independent variation of characters. It was shown in a previous section that the depth of the fork is a character that is closely related to the relative length of the tail. Also that there is a loose correlation (with many exceptions) between general size and length of the tail. Some of the most specialized features, however, do not appear to be correlated with other characters. Among the crested drongos only *D. paradiseus* is racket-tailed, not the three other species. Of the two racket-tailed species, one is large-sized, crested, and has spangles and

hackles; the other is of medium size, not crested, and has high metallic gloss. It therefore seems that—except for proportions—there is relatively little correlation between the morphological specializations of the various species of drongos.

III. Geographical Variation

Every interspecific difference ("species character") within the drongo family is known to vary also intraspecifically (by geographical variation), with the exception of the number of tail feathers. An analysis of the geographical variation of the taxonomic characters of this family is thus necessary in order to shed additional light on the origin of taxonomic differences and the rules according to which they vary.

Size

As stated above, most species of the family are very similar in size, the mean of the wing length of adult males varying between 130 and 150 mm. The smallest species (*ludwigii*) has a mean of 107, the largest (*megarhynchus*) of 184 (fig. 2). All but seven of the twenty species show geographical variation of size. Most of the seven non-variant species are restricted to a single island (*megarhynchus, montanus, fuscipennis, waldenii,* and *aldabranus*); only two are continental (*annectans, atripennis*). The greatest span of size variation is found in two species. The mean wing length of adult males in various subspecies of *D. hottentottus* is as follows: 134, 135, 136, 140, 141, 142, 145, 146, 148, 149, 149, 151, 152, 152, 156, 160, 161, 166, 169, 172, 172, and 175. The range of variation in closely related *paradiseus* is nearly as great, ranging from 142 in the smallest to 180 in the largest race (Vaurie, 1948). The geographical variability within these two species thus spans most of the size range of all the species of the family.

Pigmentation

The color of the body plumage varies geographically in several species of drongos. This variation will be discussed in a later section, since most of it appears to be closely correlated with the humidity of the environment. The only case where no such correlation seems probable occurs in the species *balicassius* which is all black in most of its range in the northern Philippines, but has a race with a pure white belly on the islands of the Visayan group (*mirabilis*).

The iris is brown in most birds, but it may also be red, yellow or (bluish) white, particularly in black birds (crows, grackles). It is brown in all immature drongos and red in the adults of most species. In *D. hottentottus* an interesting case of geographical variation of iris color occurs (fig. 4), to which Stresemann (1939) first called attention. All the eastern races have a red iris, but in the western group the iris may be either white or brown. In the series of closely related subspecies that spread from Obi to the west Sumatran islands the iris color varies as follows: *guillemardi* (Obi) (brown)→*pectoralis* (Sula) (red)→*leucops* (Celebes) (white)→*jentinki* (Kangean, Bali) (white)→*viridinitens* (Mentawei) (red). This shows the instability of iris color in this line. The same group when colonizing Borneo from Celebes reverted from white to red and then again to red-brown and brown on the Asiatic continent.

Proportions

Not only general size, but even more so proportions are subject to geographical variation. In the drongos, this is most evident in regard to the length of the tail, less so in regard to the bill.

Geographical variation of relative length of the tail. This character, referred to as "tail-index" in the subsequent discussion, is measured as the length of the outermost (longest) tail feather in per cent of wing length. This index may rise above 100, since the tail is occasionally longer than the wing. As stated above, the tail-index is consistently high in some species (e.g., *D. macrocercus*), but it

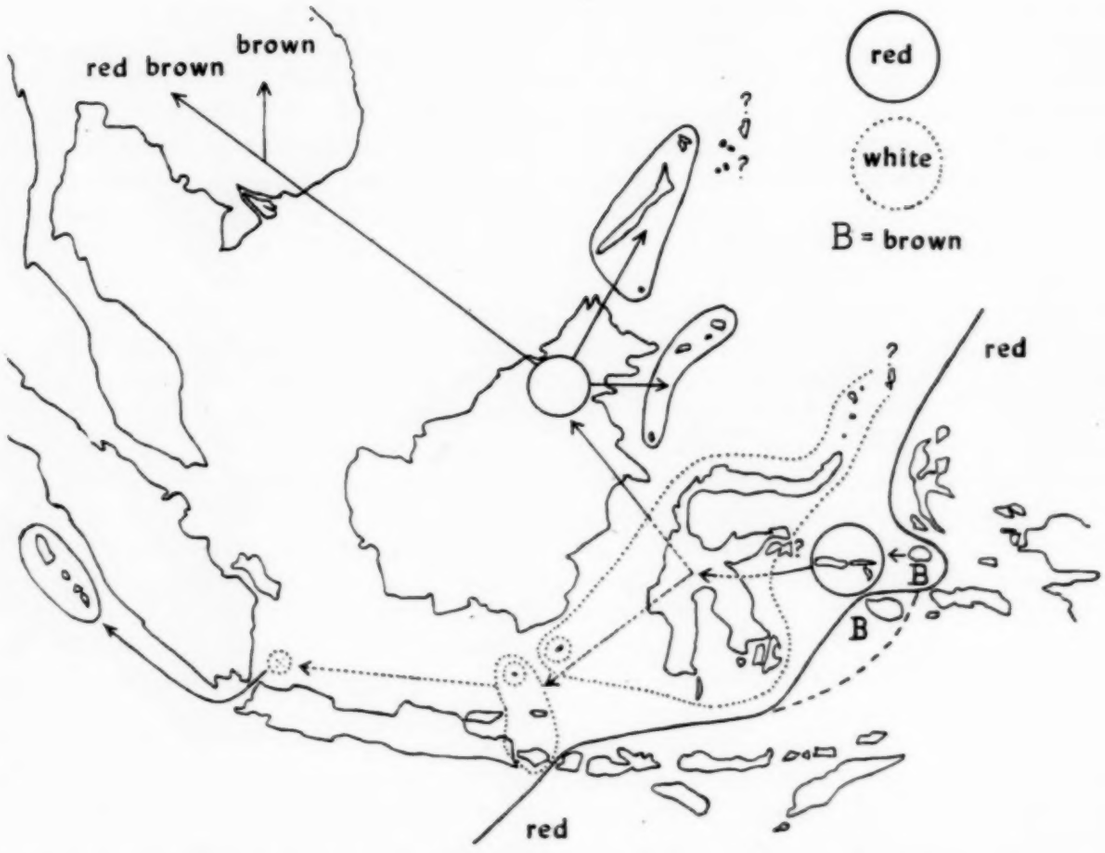

FIG. 4. Geographical variation of iris color in the western waves of *Dicrurus hottentottus*. Populations with a white or brown iris have descended from red-eyed birds and have given rise to red-eyed birds. All eastern subspecies have a red iris.

tends to vary geographically in most polytypic species of drongos.

In the superspecies *adsimilis* the tail is short (79–93) in all the subspecies of continental Africa and in *fuscipennis* (88) of Grand Comoro. It is slightly longer in *D. a. modestus* of Principe Island (88–96) and decidedly lengthened on some of the islands of the Mascarenes: *forficatus* (Madagascar) 97.5–107.0, *aldabranus* (Aldabra Island) 96.0–101.5, and *waldenii* (Mayotte) 140.

In *macrocercus* of Asia there is a conflict between the trends in the western and eastern portion of the range of the species. In the west, the Himalayan race *albirictus* has the longest tail (111), the peninsular Indian form a smaller one (108), and the Ceylon bird the smallest (105). In the east the northern races, *cathoecus* (China, etc.) and *harterti* (Formosa), have short tails (94–105), while the tropical races from south Siam and Java have long tails (117–124).

In *leucophaeus* all eastern populations, whether tropical or not, have short tails (85–100); tail length increases in the populations of northern Indo-China (Siam, Burma, etc., *mouhoti* [97.5–109.0] and *hopwoodi* [98.0–112.5]), and reaches a peak in the Indian-Himalayan populations: *longicaudatus* (105–124) and *beavani* (109–116). There is thus a clinal increase in tail size from the Malayan populations through Siam and Burma to the Himalayan population. There is no correlated increase of general size. However, what is more interesting is, as mentioned, that in this same species there is *no* clinal change of tail length in the series of populations that extend from Malaysia

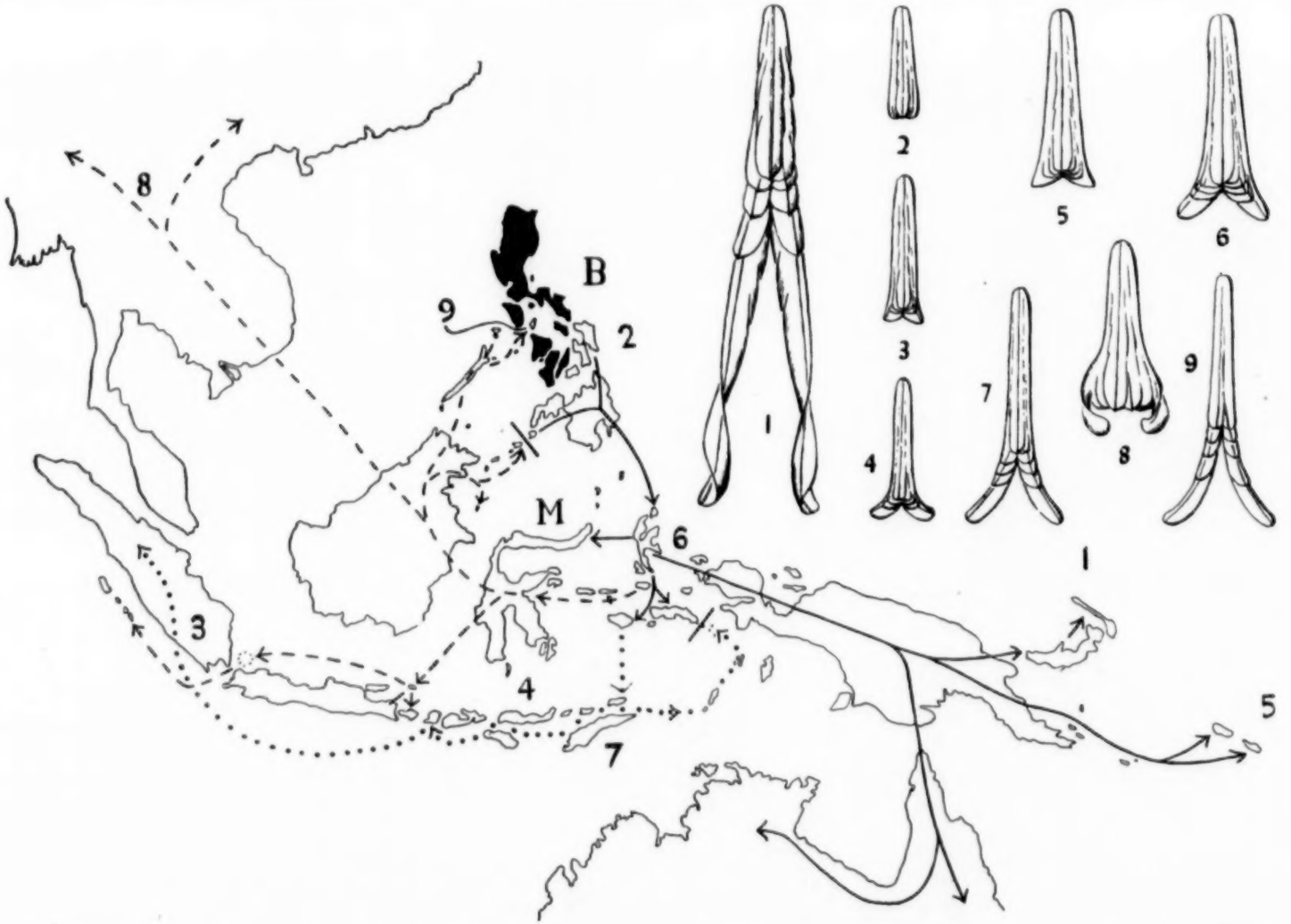

FIG. 5. Branches of the polytypic species *Dicrurus hottentottus*. Solid line: group 1(A) (oldest); dotted line: group 2(B); broken line: group 3(C) (most recent). B = closely related species *D. balicassius* in northern Philippines. M = *D. montanus*, the product of a double invasion of *hottentottus* on Celebes.

The figures on the map indicate the ranges of the 9 forms, the tails of which are shown in the insert. 1 = *megarhynchus* (New Ireland), 2 = *samarensis*, 3 = *sumatranus*, 4 = *renschi* (Sumbawa), 5 = *longirostris* (San Cristobal), 6 = *atrocaeruleus* (Halmahera), 7 = *densus* (Timor), 8 = *hottentottus* (S.E. Asia), 9 = *menagei* (Tablas). The tails of 4 and 6 are typical for the species, the tails of the peripheral forms 1–3, 5, 7–9 are aberrant and specialized in various directions.

in the south through Indochina, south China to north China.

The most complicated picture of geographical variation of tail length is found in *Dicrurus hottentottus* (fig. 5). In Group A which is made up of the oldest forms of the species, the wing-tail index is most variable. The range of variation is enormous, from a low found among the forms of the southeastern Philippines, *samarensis* (Samar and Leyte) 66.0–71.0 and *striatus* (Mindanao) 74.0–83.5, to a high found in another peripheral member of the superspecies, *D. megarhynchus* (New Ireland) with 202.0–213.0. In this group the wing-tail index increases above the Philippine low as the Moluccas are reached with *morotensis* (Morotai) 90.0, this figure holding fairly constant throughout the Moluccas, *atrocaeruleus* (Halmahera) 87.0–95.0, *manumeten* (Seran) 87.0–91.0, *amboinensis* (Amboina) 90.0–94.5. The New Guinea race (*carbonarius*) 84.0–97.5 is similar to that of the Moluccas, while that of Australia (*bracteatus*) has a slightly shorter tail, 76.5–89.5.

In Group B there is much less variation, that is within each of the two branches; in the eastern branch the wing-tail index is consistently large, 104–112.0 in *buruensis* (Buru), 111.0–114.0 in *densus* (Timor), 98.0–100.0 in *kühni* (Tenimber), and 100.0–103.0 in *megalornis* (Kei). In the western branch of Group B the wing-tail index follows a perfect clinal decrease, in the easternmost race of this branch, *sumbae* (Sumbae), the index is 95.0–100.5, in Flores (*bimaënsis*) 82.5–90.0, in Sumbawa (*renschi*) 78.0–82.5, ending with 69.5–71.5 in Sumatra (*sumatranus*). That this is not paralleled by a general decrease of size is shown by the wing length of these forms, *sumbae* 143.0–154.0, *bimaënsis* 141.0–147.0, *renschi* 132.5–136.5, *sumatranus* 149.0–153.0. The last named form is the largest, but it has the relatively smallest tail.

In Group C of *hottentottus* the relative length of the tail is uniformly smaller than in the other two groups, and there is little variation from race to race, with the exception of the three races from the southwestern Philippines with an index of 116.0–134.0 in *menagei* (Tablas), 83.0–94.0 in *palawanensis*, and 84.0–91.0 in *cuyensis*. The other races of Group C average from 78.0–85.0, rising up to 90.5 in the Himalayan race (*chrishna*).

The Crest

Several authors have assigned considerable taxonomic importance to the presence of a crest and its special configuration. In fact, it has been used in several generic diagnoses and has formed the basis for separating *D. hottentottus* specifically from *D. bracteatus*. It is therefore very instructive to follow the geographic variation of crest structure in the two species, *hottentottus* and *paradiseus*.

D. hottentottus. None of the twenty-one forms of groups 1 and 2 (waves A and B) of the species have the feathers of the forehead modified into filaments or crest feathers. Such modifications are found only in group 3 (Vaurie, 1948). In *guillemardi* (Obi) about half the adults have on the forehead hair-like filaments of medium length which curve back over the head. All the related races have a tendency for such filaments although they are absent in a few populations. The incidence of filaments is about as follows: *guillemardi* (Obi) (50 per cent), *leucops* (Celebes) (20 per cent), *jentinki* (Java Sea) (75 per cent), *pectoralis* (Sula) (50 per cent), *borneensis* (Borneo) (100 per cent), *suluensis* (Sulu) (100 per cent), *palawanensis* (Palawan) (0 per cent), *viridinitens* (Mentawei Island) (0 per cent).

In these forms the filaments (if present) are short or medium-sized, and may be either present or absent even in closely related populations. In the *hottentottus* subgroup the filaments are considerably longer and present in all the forms. Their length in millimeters is: *hottentottus* 61–114 (83), *brevirostris* 62–106 (83), and *chrishna* 60–106 (85). There is a tendency in some of the adults, particularly of

FIG. 6. Geographical variation of length of crest in *D. paradiseus*. 1 = *brachyphorus*, 3 = *microlophus*, 4 = *platurus*, 5 = *formosus*, 6 = *hypoballus*, 7 = *paradiseus*, 8 = *rangoonensis*, 9 = *grandis*, 10 = *johni*, 12 = *lophorinus*. Note increase from the small Bornean (1) to the large Himalayan (9) subspecies.

brevirostris, to have the proximal half or third of the frontal filaments partially and finely barbed rather than bare. This beginning of a crest is not evolved any further in the species *andamanensis* which has only a few hairs (15–20 mm.). A true crest is, however, developed in the closely related species *D. paradiseus*.

Evolution of the crest in D. paradiseus. The evolution of the crest in drongos reaches its peak in *D. paradiseus*, but interestingly enough within this one species every stage is found from entirely uncrested subspecies at one end to fully crested forms at the other (fig. 6). The crest reaches its greatest length (54–66 mm.) in the Himalayan form *grandis*. This crest is formed by a dense tuft of fully webbed feathers that spring from the base of the bill and curl backward toward the crown. From this the length of the crest decreases regularly along two clines. One of these, through the Indian Peninsula, reaches its end on Ceylon, where *lophorinus* has only a short crest (9–15) although it still typically consists of fully webbed feathers. The other cline runs southward through the Indochinese countries to Malaya. Around Penang it has reached the same level in the subspecies *hypoballus* (12–22) as on Ceylon. From there to the tip of the Malay Peninsula it becomes reduced still further until it is a mere tuft or is occasionally missing altogether. The proportion of such crestless individuals greatly increases in Sumatra, and on the western Sumatran islands the crest has degenerated to the point where it can no longer be measured even in the few "tufted" individuals.

Variation on the islands, however, is quite irregular. On Hainan the crest (47–57), though a little shorter than in the Himalayan *grandis* (54–66), is, if any-

thing, even more striking, for the feathers are considerably broader and more curly. The crest is well developed on the Nicobars (*nicobariensis*), but is rudimentary or lacking in the Andamans (immediately south of the Nicobars), in the Natunas, Anambas, as well as on Borneo. However, it reappears again in Java (*formosus*).

Tail Rackets

Terminal tail rackets are present in the adults of two only distantly related species, *remifer* and *paradiseus* (fig. 2).

All the races of *paradiseus* normally have the tail racket except *lophorinus* (Ceylon) in which the tail is fully webbed. The length of the racket follows, on the whole, a similar cline as the crest. The longest racket of any continental population is found in *grandis* (Himalayas) (96–112), the shortest in the Malay Peninsula (60–87) and in Borneo (44–57). On the islands the variation again is irregular. On the Andamans the racket is large (88–107) and smaller in the Nicobars (75–81). In the Anambas and Natunas the racket (84–92) is rather large. Java is exceptional as with the crest, by having a population with large tail rackets (90–108). A single Java bird had the abnormally large racket of 126. The size of crest and racket in *D. paradiseus* is correlated with general size, except for the small-sized Java race (*formosus*) with large crest and racket.

The evolution of the racket in *D. remifer* has followed entirely independent lines. In the first-year birds there are no rackets, the tail being normally forked. In the second-year plumage the outer pair of rectrices becomes prolonged, the shaft is denuded, and ends in bilateral terminal rackets. However, traces of barbs persist on the wire-like shaft. In the third-year plumage, the outer pair of rectrices is still longer and all traces of barbs have disappeared from the denuded shaft. The geographical variation in this species consists in the degree of denudation. In *D. remifer tectirostris* from India and Burma, the racket starts abruptly from the shaft and as a result the bare shaft is longest, in ad. ♂ 215–306 (253.0). In *D. r. remifer* from Java and Sumatra, the racket tapers a little onto the shaft, and as a result the bare part of the shaft is shorter, ad. ♂ 150–246 (205.71). Interestingly enough, the birds in the intervening regions of the Malay Peninsula from Tenasserim down to Selangor (*peracensis*) and those in the mountains of southern Cambodia (*lefoli*) are not intermediate. Rather their rackets are extremely long, more ribbon- than racket-like. It appears as if an "immature" character had persisted in the otherwise fully adult bird. In *peracensis* the bare shaft is only 105–268 (171.72) and 125 in *lefoli*. The degree of denudation is not associated with the total length of the feather, for this feather is 432–532 (475.0) in *tectirostris*, 392–453 (429.8) in *remifer*, 374–514 (468.9) in *peracensis*, and 580.0 in *lefoli*. The bird with the longest feather has the shortest bare shaft.

IV. Environment and Geographical Variation

Numerous cases were quoted in the preceding section which illustrate the phenomenon that nearly every taxonomic character that varies between species of drongos (interspecific differences) also varies geographically (intraspecifically). It shall be pointed out in the present section that much of this variation is not haphazard, but correlated with the geographically changing environment. Such geographical variation can be referred to equally well as ecological variation. Many of the known regularities of this variation have been formulated as the so-called ecological rules, such as Bergmann's rule, Gloger's rule, Allen's rule, etc.

The morphological responses of warm-blooded (endothermal) and mobile vertebrates to the changes of the environment are not nearly so conspicuous as those found in stationary plants, hence the emphasis of the taxonomist of higher vertebrates on geographical races (with ecological features) and of the plant tax-

onomist on ecotypes (that are geographically segregated). Actually there is no difference of kind between such animal and plant populations, but only one of emphasis of the geographical versus the ecological aspect of local populations. The present section will be devoted to an exposition of the correlation between environment and certain subspecific characters among drongos.

Temperature

Size variation within species of warm-blooded vertebrates often obeys Bergmann's rule, which states that body size increases with a decrease of the outside temperature, or expressed differently, subspecies of higher latitudes are larger than such of lower latitudes. Wing length is again used as index of size for testing the validity of this rule among the drongos.[1]

An effect of temperature on size is, of course, absent in species that are either restricted to a single island or that live on the continent in a single, restricted climatic zone (e.g., *atripennis, annectans*). All other species of drongos show variation of wing-length correlated with latitude. In *adsimilis* there is a regular cline of decreasing size, reaching a minimum in tropical east Africa (Vaurie, 1948), but this cline is not nearly so steep as the clines in the various Indian species. All Indian species follow typical clines from the Himalayas in the north to south India and Ceylon on one hand, and to Burma and Malaya on the other (table 2).

This table merits some comments. All three species that live on Ceylon have developed endemic populations that are smaller than those on the Indian Peninsula. Furthermore, the populations of the dry zone of northern Ceylon, which are exposed to pronounced seasons, are of larger size than the populations of the wet zone of southern Ceylon with its more equable climate.

Noteworthy is the parallelism in the decrease of size east and west of the Bay of Bengal. In two cases (*hottentottus, paradiseus*) this parallelism is so perfect that the populations on the peninsula of India cannot be separated by any known test from the birds that occur in the corresponding climatic zone of Burma and Siam.

Finally, attention must be called to the Chinese races of *D. leucophaeus*. Although the northernmost of these races (*leucogenis*) ranges as far north as Manchuria, it is no larger than the race (*salangensis*) of subtropical China. The size variation from north to south is as follows:

D. leucophaeus (Wing length of adult males)
- North China (*leucogenis*) 138–148 (142.8) [Migratory]
- South China (*salangensis*) 139–145 (143.0) [Partly migratory]
- Central and South Siam (*bondi*) 128–138 (132.9)
- Borneo (*stigmatops*) 127–134 (129.4)

The absence of a continuation of this cline in north China may be correlated with the fact that the northern populations are migratory and spend the cold season in the subtropical and tropical parts of eastern Asia. It has been observed in North America and Europe also that migratory birds are less subject to geographical variation of size than sedentary ones.

Size Variation on Islands

Populations of a species that live on islands often differ in body size from the populations on the nearest mainland. Frequently the difference is large enough to be recognized as a subspecific difference. Such island races may be either of larger or of smaller size than the main-

[1] Size and wing length are closely correlated in birds. Yet it is known that wing length increases more rapidly than general size in migratory and certain mountain birds. It also seems that in some long-tailed species of birds the growth factors that control the lengthening of the tail may also affect the wing. It would therefore be most desirable to replace wing length by weight or some other more reliable index of general size (see Amadon, 1943), but sufficient weight data are not yet available.

land race, depending largely on the climate of the respective island (Mayr, 1942, p. 38).

The endemic races of Ceylon are smaller than those of peninsular India (see above), the races of Principe Island (off western Africa) and of Formosa (off south China) are larger than those of the opposite mainland (see table 3). Also large are the Mascarene representatives of *D. adsimilis* (130): *D. fuscipennis* (147) of Grand Comoro, *D. aldabranus* (134) of the Aldabras, and *D. waldenii* (147) of Mayotte Island.

It is sometimes stated that in the tropical zone populations of warm-blooded vertebrates that are found on small islands are of larger size than related populations

TABLE 2. Clines in the size of Asiatic drongos

Wing lengths of adult males

Dicrurus macrocercus

Himalayas (*albirictus*) 146–159 (153.0)

Indian Peninsula (*macrocercus*) 139–149 (139.6)
Ceylon (*minor*) 131.0

Formosa (*harterti*) 145–158.5 (152.2)
Burma, north Siam (*cathoecus*) 142–150 (146.0)
Central and south Siam (*thai*) 142.0
Java, Bali (*javanus*) 130–138 135.6

D. leucophaeus

In the west	In the east
Western Himalayas (*beavani*) 137–147 (141.2)	Eastern Himalayas (*hopwoodi*) 135–153 (145.3)
*Indian Peninsula (*longicaudatus*) 128–146 (135.9)	Central Burma, north Siam (*mouhoti*) 134.5–147 (139.8)
	Central and south Siam (*bondi*) 128–138 (132.9)

* Adult females included.

D. caerulescens

Northern India (*caerulescens*) 120–135 (127.5)
Southern India (*caerulescens*) 119.5–129 (122.4)
Ceylon, dry zone (*insularis*) 125.5
Ceylon, wet zone (*leucopygialis*) 120–121 (120.5)

D. aeneus

Himalayas (*aeneus*) 119–131 (123.25)

Southern India (*aeneus*) 112–122 (118.0)

Formosa (*braunianus*) 128.5–136 (132.2)
Hainan (*aeneus*) 123–130 (125.0)
North Burma (*aeneus*) 119–131 (123.25)
South Burma, Malay Peninsula to 4° N.L. (*aeneus*) 118–127 (122.6)
Malay Peninsula, south of 4° N.L. (*malayensis*) 104–116
Sumatra (*malayensis*) 105–112 (109.0)

D. hottentottus

Himalayas (*chrishna*) 168–180 (173.6)
Southern India (*hottentottus*) 165–167 (166.0)
Siam (*hottentottus*) 160–171 (166.0)
Borneo (*borneensis*) 141–149.5 (145.25)

D. paradiseus

In the west	In the east
Himalayas (*grandis*) 173–177 (175.0)	E. Himalayas and north Burma (*grandis*) 175–185 (181.25)
Central India (*rangoonensis*) 165–175 (169.3)	Northern Siam (*rangoonensis*) 163–172.5 (168.5)
Southern India (*paradiseus*) 153–162 (156.5)	Central and south Siam (*paradiseus*) 154–167 (160.2)
Ceylon, dry zone (*ceylonicus*) 150–156 (152.25)	
Ceylon, wet zone (*lophorinus*) 140–150 (145.7)	Malay Peninsula, south of 11° N.L. (*hypoballus*) 144–152 (147.6)

TABLE 3. Wing length of adult males

	Island	Adjacent mainland
D. adsimilis, Principe Island	134–141 (138.61)	130–140 (134.29)
D. aeneus, Formosa	128.5–136.0 (132.18)	112–131 (122.4)
D. macrocercus, Formosa	145–158.5 (152.18)	142–150 (146.0)

on large islands. To a limited extent this rule holds for the drongos. In *D. leucophaeus* all the populations on small islands are of larger size than the populations (or subspecies) on the larger islands from which the small islands were colonized (table 4). The rule does not hold in *D. hottentottus* where the number of exceptions to this rule is about as large as the number of confirmations. In table 5 a number of island populations of *D. hottentottus* are compared with the parental population from which they were originally derived.

TABLE 4. *Size of island and wing length in* D. leucophaeus

Large island from which small island was colonized	Small island
Sumatra (129)	Sipora (139.4)
Sumatra (129)	Siberut (137.7)
Java (133)	Simalur (135.4)
Sumatra (129)	Java (133)
Java (133)	Lombok (138)

Bill Size

In many species of birds there is geographical variation of the bill in conformance with Allen's rule, which states that appendages become relatively shorter in cooler climates. Most species of drongos do not seem to obey this rule, insofar as the bill is concerned. Rather there is a conflict between this rule and a tendency for an allometric increase of bill length with increasing size. Allen's rule is best illustrated in *D. leucophaeus* in which the northern races have approximately the same wing length as the tropical races. The bill index (length of culmen in per cent of wing length) is lower [18.26, 18.32] in the two races of subtropical and temperate China (*leucogenis* and *salangensis*) than in any of the races from the tropical parts of the range (19.15–20.90).

On the other hand, in the western group of *leucophaeus* and in *paradiseus* the relative length of the bill remains the same in the cooler climate (table 6).

Humidity

It has been known for more than a century that humidity of the environment affects pigmentation. The intensity of melanins in particular tends to be greater in the more humid parts of the range of species. In glossy black birds this rule can be extended by the statement that the gloss tends to be of a deeper, more bluish or purple color in humid districts, and of a less saturated, more greenish color in the more arid districts. This holds among the drongos for *ludwigii, adsimilis, hottentottus, carbonarius,* and *balicassius.* In *caerulescens* the darkest subspecies is *leucopygialis* from the wet zone of Ceylon, the lightest is *caerulescens* from the rather arid Indian Peninsula.

In some cases the geographical variation of pigmentation appears wholly cap-

TABLE 5. *Inverse correlation between size of island and body size in* Dicrurus hottentottus

Correlation valid
- Mindanao (134.7) to smaller northern Moluccas (172)
- Northern Moluccas (172) to larger New Guinea (152)
- Northern Moluccas (172) to larger Seran (141)
- Seran (141) to smaller Buru (154)
- Seran (141) to smaller Ambon (149.5)
- Timor (155.8) to smaller Tenimber (161)
- Palawan (141.8) to smaller Cuyo (152.9)

Correlation not valid
- Morotai (148.5) to larger Halmahera (172)
- Sula (151.2) to larger Celebes (163)
- Buru (154) to larger Timor (155.8)
- Lombok (144.7) to larger Sumatra (152)
- Borneo (145.2) to smaller Palawan (141.8)

In each case the parental population is listed first, the derived population second. Figures in parenthesis indicate mean wing length of adult males (from Vaurie, 1948).

TABLE 6. *Bill size and climate (adult males)*

	Wing length	Bill length (mean)	Bill index
D. leucophaeus			
Eastern Himalayas (*hopwoodi*)	135–153 (145.3)	28.4	19.6
Western Himalayas (*beavani*)	137–147 (141.2)	26.9	19.1
Northern Siam (*mouhoti*)	134.5–147 (139.8)	27.1	19.4
Central Siam (*bondi*)	128–138 (132.9)	25.7	19.4
D. paradiseus			
Eastern Himalayas and north Burma (*grandis*)	175–185 (181.2)	41.2	22.7
Central Burma, northern Siam (*rangoonensis*)	163–172.5 (168.5)	37.0	22.0
Central and northern Siam (*paradiseus*)	154–167 (160.2)	34.8	21.7
Malay Peninsula (*hypoballus*)	144–152 (147.6)	33.4	22.7

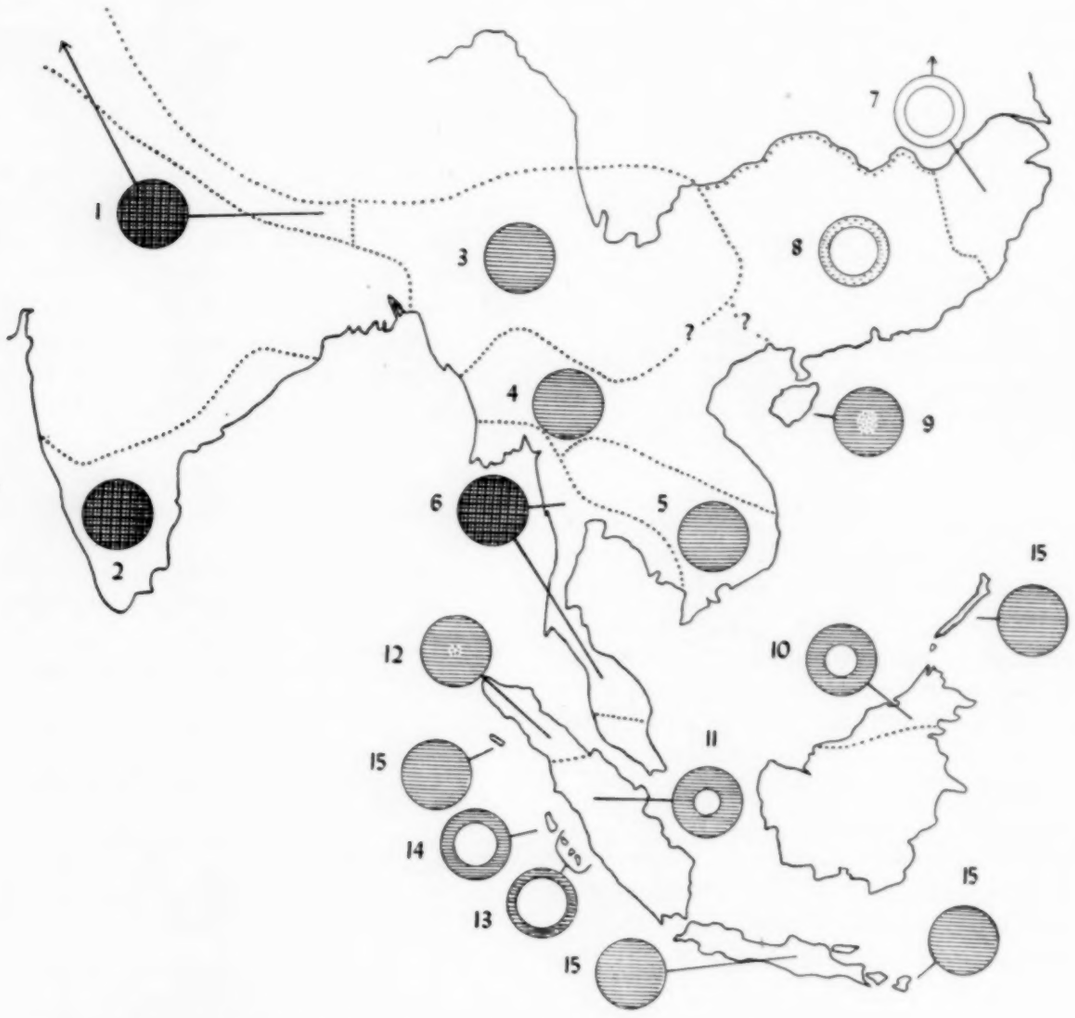

FIG. 7. Geographical variation of intensity of pigmentation in *D. leucophaeus*. The lightest subspecies are 7 and 8, the darkest, 1, 2, and 6. The size of the white center on 7–14 indicates the amount of white on the sides of the head. 1 = *beavani*, 2 = *longicaudatus*, 3 = *hopwoodi*, 4 = *mouhoti*, 5 = *bondi*, 6 = *nigrescens*, 7 = *leucogenis*, 8 = *salangensis*, 9 = *innexus*, 10 = *stigmatops*, 11 = *phaedrus*, 12 = *batakensis*, 13 = *periophthalmicus*, 14 = *siberu*, 15 = *leucophaeus* (divided range).

ricious, as in the case of the Mascarene species of superspecies *D. adsimilis* and of the subspecies of *D. leucophaeus* (fig. 7).

In *leucophaeus* the darkest races are the two races from the Indian Peninsula and the Himalayas, the two palest races those from China. Borneo (*stigmatops*) is a fairly light center from which three lines of subspecies radiate, all of which darken in a parallel manner (1) toward Palawan, (2) through south Sumatra and Java to Lombok, and (3) through south and north Sumatra to Simalur and the Malay Peninsula. In these three lines there is not only a general darkening of the body plumage, but also a reduction or complete obliteration of the white facial mask. The result is that polyphyletically three populations have evolved, (1) on Palawan, (2) on Java-Bali-Lombok, and (3) on Simalur, that have become so similar that they cannot be distinguished taxonomically. As stated, all this variation appears exceedingly capricious, but a thorough analysis of climatic conditions may yet establish an environmental correlation.

If there are many exceptions among subspecies of a single species in regard to the correlation between degree of pigmentation and humidity of the habitat, this is even more true for species. The grayest of the Indian drongos, *D. caerulescens*, is much more a bird of the forest than some of the glossy black species (e.g., *D. macrocercus*) that occur in the same general region.

Clines

Where features of the environment change gradually over a wide geographical area, a corresponding gradual change of taxonomic characters often evolves. Such character gradients, called clines by Huxley, are very common in species of the drongo family. They occur in all the widespread continental species.

Clines in general size (wing length) occur in *D. adsimilis* and *D. ludwigii* in Africa and the species of continental Asia (see above). In all these species clines are also found concerning the size of the tail, the relative size of the tail, the depth of the fork in the tail, and the relative length of the bill (see above). The intensity of pigmentation changes in form of a cline in parts of the range of *D. leucophaeus* (fig. 7) and in *D. caerulescens*.

The strict correlation between environment and cline formation is most conspicuous in the parallel clines that develop in *D. paradiseus, D. hottentottus,* and *D. leucophaeus* on both sides of the Bay of Bengal, in the Indian Peninsula in the west and in Burma-Siam in the east (table 2).

In addition to these orthodox clines that appear to be due to parallel gradients of factors of the environment there seems to exist a different type of clines termed "progressive clines" by Braestrup (1945). This author points out that character progressions are often found in allopatric populations which are analogous to the vertical sequences of the paleontologist. The cline of crest length in *D. paradiseus* from the Malay Peninsula through Burma to the Himalayas (fig. 6) is a splendid example of such a "progressive cline," corresponding to an evolutionary series. In this case it is probable that the cline is due in a large measure to allometric growth (table 7). In other words, the cline of crest length is indirectly the result of the cline of increasing size, which in turn conforms to Bergmann's rule. Braestrup points out that most of the progressive clines are due to similar selective gradients of the environment.

However, it appears doubtful whether this explanation is applicable in all cases. The species *hottentottus*, which is widespread in the Indo-Australian archipelago, consists of three or four well-defined "colonization waves" (Vaurie, 1948) (fig. 5). There are very regular character progressions along these colonization routes, *even though there is no evidence for parallel environmental changes.* Such character gradients are evident in the lines: Samar-Mindanao - Morotai - Halmahera - New Guinea-New Britain-New Ireland, or Se-

TABLE 7. *Increase of crest length with size in* D. paradiseus (adult males)

	Wing length	Crest length
brachyphorus (Borneo)	138–147 (142.6)	None
hypoballus (Malay Peninsula)	144–152 (147.6)	12–22 (15.5)
paradiseus (south and central Siam)	154–167 (160.2)	15–32 (24.7)
rangoonensis (central Burma, northern Siam)	163–172.5 (168.5)	31–55 (42.5)
grandis (north Burma, eastern Himalayas)	175–185 (181.25)	54–70 (58.3)

ran-Buru-Timor-Tenimber-Kei, or Seran-Buru-Timor-Sumba-Sumbawa-Lombok-Sumatra, or Buru-Sula-Celebes-Borneo-Palawan-Cuyo-Tablas. Similar progressive changes along routes of expansion (often loosely referred to as routes of migration) have been described also for *Rhipidura rufifrons* (Mayr and Moynihan, 1946).

The correct interpretation of these chains of intergrading populations faces some difficulties. It may be observed that the changes within these series of neighboring populations are not always rectilinear. Size, for example, is repeatedly increasing and decreasing in various of the above listed "waves" of *D. hottentottus*. So are the various characters that are correlated with size, such as relative length of tail, depth of the fork, etc. It appears likely that the regularity of character changes along these series of island populations is to a considerable extent due to gene flow. This possibility will be discussed in connection with hybridization (see below).

Geographical Variation of Habitat Requirements

Not only morphological characters are affected by the geographical changes of the environment, but also the ecological requirements of different populations of a single species. In Africa *D. adsimilis adsimilis* and *D. a. divaricatus* are restricted to savannas, while *D. a. coracinus* is restricted to the rain forest. In Ceylon *D. caerulescens insularis* and *D. paradiseus ceylonicus* are birds of the dry zone, *D. c. leucopygialis* and *D. p. lophorinus* birds of the wet zone. The vertical distribution seems to vary geographically in *D. leucophaeus, D. macrocercus, D. hottentottus* and *D. paradiseus*, although exact data are not available. However, it is known that in Siam *D. leucophaeus hopwoodi* occurs in the mountains in the north, *D. l. mouhoti* on the plateau, and *D. l. bondi* in the south below the plateau. Three races of *D. paradiseus* are distributed in a similar manner above, on, and below the plateau: *grandis, rangoonensis*, and *paradiseus*. Such ecological plasticity is a prerequisite for wide geographical distribution. A species that lacks it, such as *D. annectans*, will be condemned to a restricted geographical range. Furthermore, such ecological differences among geographical races facilitate speciation (*D. hottentottus-montanus* on Celebes), although not necessarily preventing hybridization between previously separated subspecies. Ecologically very different subspecies of *D. caerulescens* and of *D. paradiseus* hybridize on Ceylon, and so do *D. adsimilis adsimilis* and *D. a. coracinus* in Africa (hybrid: *atactus*) (Vaurie, 1948).

V. SPECIATION

Speciation depends on the origin of discontinuities between populations. A study of speciation involves therefore a study of the structure of species in respect to the conditions under which such dis-

TABLE 8

Number of species	Number of subspecies per species
8	1
3	2
3	3
1	4
1	5
1	7
1	14
1	15
1	32
20	100

continuities between conspecific populations develop. An analysis of the structure of species is important also as a contribution to comparative systematics. It is thought that the structure of a given species is determined by its genetic structure, but also by its ecological tolerance, dispersal facilities, and sexual biology. Not enough data are available thus far to express these correlations quantitatively in terms of definite rules.

Geographic Variation

Number of subspecies. The twenty species of drongos have a total of 100 subspecies. The exact average of five subspecies per species is actually achieved only by a single species. The others have either fewer or more. The plotting of the species against the number of subspecies results in the usual hollow curve (table 8). Three species (15 per cent) thus account for 61 per cent of all the subspecies. The number of eight monotypic species seems unusually large, but only two of them are continental (*atripennis, annectans*) and two others are found in the mountains of large islands (*Chaetorhynchus papuensis, D. montanus*). The other four species are restricted to small islands (*aldabranus, fuscipennis, waldenii, megarhynchus*). Furthermore, all the island species, except one (*C. papuensis*), are members of widespread superspecies, in which geographical variation has reached species level. Geographical variation is thus almost universal among the drongos. Its absence in *atripennis* may be due to the fact that this species has a restricted range in the climatically uniform African rain forest; while the highly migratory *annectans* may lack geographical variation because the populations in its rather restricted breeding range become intermingled by migration. It is the most migratory species of drongos, except for some races of *D. leucophaeus*.

The average of five subspecies per species (or 7.7 subspecies per superspecies) is higher than the average for birds. About 28,500 subspecies are recognized in the 8600 species of birds (= 3.3 subspecies per species). This high average is largely due to the extreme geographical variability of the single species *D. hottentottus*, which with its thirty-two subspecies is one of the most variable of all birds.

The number of described subspecies by no means fully characterizes the amount of geographical variation among the drongos. There is much difference between local populations that is not worthy of subspecific recognition. Vaurie (1948) has described this for populations of *D. l. leucophaeus, D. p. paradiseus, D. p. platurus, D. h. carbonarius*, and others. In fact, there is hardly a widespread subspecies that does not break up into numerous slightly different local populations.

It is thus possible to find among the drongos every level of speciation from barely noticeable intrasubspecific populations to superspecies (*macrocercus, hottentottus*).

Rate of subspeciation. In spite of the large interest in the rate of subspecies formation, there are actually but few reliable data available. Zeuner (1943) made a detailed analysis of species and subspecies formation in the Indo-Australian butterflies of the genus *Papilio* (*Troi-*

TABLE 9. *Wing length of recent subspecies*

	Large islands or mainland	Small islands on drowned Sunda Shelf
D. paradiseus	Malaya 140–160 (148.25)	Tioman 151–162 (155.3)
D. paradiseus	Malaya 140–160 (148.25)	Anamba 165
D. paradiseus	Borneo 138–147 (142.6)	Banguey 146–158 (150.6)
D. leucophaeus	Sumatra 123–135 (129.0)	Sipora, Pagi 137–144 (139.4)
D. leucophaeus	Sumatra 123–135 (129.0)	Siberut 134–140 (137.7)
D. hottentottus	Borneo 141–149.5 (145.2)	Maratua 149–157 (152.3)
D. hottentottus	Palawan 140–143 (141.8)	Cuyo 151–155 (152.9)

des) and postulated an approximate age for the various described forms. However, he had to make so many simplifications to arrive at his figures that they have become virtually valueless. He had to ignore the fact that there are different rates of evolution in large and in small populations, that selection pressure is different on the different islands, and that there is much evidence for inter-island dispersal. The same objections could be raised against a similar analysis of the drongos. However, as Stresemann points out (1939), even though it may be impossible to determine the age of any of the species, at least the maximum age of those subspecies can be determined which are restricted to the small islands on the Sunda Shelf. These little islands, together with the adjacent larger islands, were parts of Sundaland during the recent glaciation, about 10,000 years ago. The subspecific characters must have developed since the flooding of the Sunda Shelf. Several of these "new" subspecies are listed in table 9.

There is an alternative interpretation which deserves mentioning in spite of its improbability. All these populations on the small islands show increased size. It is possible that heterosis is in part responsible for this. Strays from various neighboring mainland districts and from other islands probably reach these islands occasionally and may have a considerable genetic effect in view of the very small population size on most of these islands. Opposed to this interpretation is the fact that such hybridization will be counteracted by the homogenizing effect of the small population size.

Peripheral Populations

Granting that differentiating populations are the starting points of new species, it is very important to study the degree to which existing populations within a species have differentiated and how they are distributed. If ecological adaptation to special conditions constitutes an important method of speciation, one would expect that populations of incipient species rank might be distributed at random over the species range. However, if geographical isolation is the primary factor in speciation, the most aberrant populations should occur in various isolated locations and, in particular, along the outer periphery of the species range.

A tabulation of the more distinct subspecies of drongos shows that in nearly all cases they are isolated and peripheral (table 10). Such striking peripheral populations, however, have not evolved in all species, for example, not in the continental ranges of *D. adsimilis* and *macrocercus,* and only to a slight extent in *D. leucophaeus.* What is important is the fact that striking subspecies have not developed in the central parts of the range of any of the species, in response to some exceptional ecological conditions.

TABLE 10. *Very distinct subspecies and semispecies* in the genus* Dicrurus

adsimilis (Africa)
  waldenii (Mayotte), *fuscipennis* (Comoro), *aldabranus* (Aldabra Island), *forficatus* (Madagascar)
balicassius (Philippines)
  mirabilis (Viscayan group)
aeneus (Asia)
  braunianus (Formosa)
hottentottus (many examples, see fig. 5)
paradiseus (India-Malaysia)
  lophorinus (Ceylon), *otiosus* (Andamans), *formosus* (Java)

* Semispecies are species that are members of superspecies.

The most convincing illustrations of the rule of peripheral populations are found in the species *D. hottentottus.* The characters of exceptionally long bill (San Cristobal) and exceptionally long tail appear in populations that are peripheral. The only peripheral populations of *D. hottentottus* that have not evolved aberrant characteristics are the races on the Asiatic continent (*hottentottus,* etc.). Presumably they form too large a continuous population for the development of aberrant characteristics, thus negatively confirming again the importance of isolation.

One of the characteristics of isolated peripheral populations is the unpredictability of their variation. The New Guinea race *carbonarius* of *D. hottentottus* is medium-sized: ♂ ad. 142–162 (152). Individuals of this subspecies colonized various islands adjacent to eastern New Guinea. The resultant populations either remained of approximately the same size, *meeki* (Guadalcanal) (152) and *laemostictus* (New Britain) 141–159 (151), or became slightly smaller, *longirostris* (San Cristobal) 143–145 (148.7), but one of them developed giant size, *megarhynchus* (New Ireland) 182–186 (183.8). Exceptionally short tails developed in *hottentottus* in such distant places as the eastern Philippines, Sumatra, and Solomon Islands, exceptionally long tails in such equally scattered localities as New Ireland, Kei Islands, and western Philippines (fig. 5). Paleness in *D. leucophaeus* likewise evolved independently in a number of localities along the periphery of the range (fig. 7).

In nearly all cases where a continental species has colonized islands, it has formed there more or less pronounced subspecies. This holds for:

adsimilis (Principe Island)
superspecies *adsimilis* (Mascarene Islands)
aeneus (Formosa)
macrocercus (Ceylon, Formosa, Java)
leucophaeus (Hainan, Greater Sunda Island)
caerulescens (Ceylon)
paradiseus (Java, Borneo, Ceylon, Hainan).

It does not hold for *aeneus* as far as the Greater Sunda Islands are concerned. In *D. remifer* the most distinct subspecies are on the isolated mountain ranges of south Indochina.

A few species have not invaded any islands and these are characterized by having very few or slight subspecies: *ludwigii* (2), *atripennis* (1), *annectans* (1), and if New Guinea is considered as continental: *Chaetorhynchus papuensis* (1). Two species occur on islands that are situated on the continental shelf, without having speciated noticeably: *D. aeneus* and *D. remifer*.

These facts can be summarized in the statement that isolation, either on islands or along the periphery of the range, is a powerful stimulus toward the development of aberrant populations. In combination, the two factors are particularly potent, as illustrated by the species *Dicrurus hottentottus*.

Borderline Cases

The family is replete with forms that are on the borderline between subspecies and species. They occur in seven of the thirteen species or superspecies. To begin with, the two superspecies, *adsimilis* (6 species) and *hottentottus* (3 species), are borderline cases themselves. They are composed of species that are not only closely related but also geographically representative. These species, although clearly revealing their origin by geographical speciation, are now sufficiently distinct to be considered full species.

Furthermore, there are subspecies in seven species, *ludwigii, adsimilis, leucophaeus, balicassius, remifer, hottentottus,* and *paradiseus,* which are so distinct that they were considered as separate species even by recent authors. Vaurie (1948) has discussed in detail the previous treatment of the forms included in these species, as well as the reasons why they should be considered as conspecific. If morphological distinctness and absence of intergradation were accepted as the only species criteria, the number of species among the drongos would have to be raised to more than twice the number of twenty admitted at present.

The danger of overestimating the value of morphological criteria becomes clear to anyone who tries to assign taxonomic rank to drongo populations. It is very evident that the same degree of visible morphological difference between populations may have very different taxonomic value in different cases. The more prim-

itive species of *Dicrurus* (e.g., *ludwigii, atripennis,* and *adsimilis*), for example, show only very slight differences in size, amount of gloss, and shape of tail. Much greater differences are found between populations of the more specialized species (e.g., *hottentottus, paradiseus*) that obviously deserve only subspecific rank. Too great a reliance on morphological criteria would lead to wrong ranking of these populations.

Double Invasions

Under this term we understand the repeated invasion of an island by colonists of the same parental stock coming from the mainland or from some other island. If the interval between the two invasions has been long enough to permit the development of isolating mechanisms, the second wave of colonists will live side by side the first wave as a good species.

The overlap of *D. montanus* and *D. hottentottus leucops* on Celebes is the result of a double invasion. *D. montanus* is clearly the earlier arrival. It is a descendant of the stock that came from Mindanao (*striatus*) and produced *morotensis* and *atrocaeruleus* in the northern Moluccas. Though this relationship is very clear, it can no longer be determined whether *montanus* is the result of a colonization directly from Mindanao or indirectly via the northern Moluccas. The second wave of *hottentottus* to reach Celebes arrived at a much later date, via Seran-Buru-Sula Islands, as an analysis of the morphological characters clearly indicates (Vaurie, 1948). This second colonization produced *D. h. leucops*. Plotted on a large-scale map the ranges of *montanus* and *leucops* on Celebes almost exclude each other. However, this pseudogeographical representation is due to differences in the ecological requirements. *D. h. leucops* is a bird of the lowlands and of the more open country up to 1200 meters, only occasionally in the true forest, while *D. montanus* is a forest bird and prefers higher altitudes (500–1800 m.). However, since there are no signs of interbreeding in the forest at the lower altitudes where the two forms occasionally come in contact, they must be treated as separate species. It is interesting that here again, as in so many similar instances, the earlier immigrant inhabits primeval forest while the later immigrants inhabit secondary habitats (second growth, open country, etc.).

The second case of successful double invasion among the drongos is not nearly so clear cut. On the Andaman Islands there is an endemic species of drongo, *D. andamanensis,* which in many of its characters is close to some races of *paradiseus,* although lacking the tail rackets. In that respect and in others it resembles *D. paradiseus lophorinus* of Ceylon, though it is more likely that it descended from *D. p. hypoballus* (Malay Peninsula). Also on the Andaman Islands is found *paradiseus otiosus,* the result of a second colonization.

In island birds the second "wave" normally consists only of a few pioneers who gradually build up into a new subspecies or species, provided they are protected by reproductive isolation against absorption by the descendants of the first wave of immigrants.

Hybrid Populations

On continents and large islands hybrid populations may develop when populations come together again that had previously been segregated without developing complete reproductive isolation. This occasionally involves populations that had attained a considerable degree of morphological distinctness. Such hybrid populations often develop after the breakdown of a previously existing geographical or eco-geographical barrier, and it is therefore not surprising that several species may develop hybrid populations in the same zone, as pointed out by Meise (1928). Such zones are situated, for instance, along the edge of the African rain forest (Chapin, 1948) and on Ceylon, where dry zone and wet zone meet (Ripley, 1946). The details of the structures of these hybrid populations among the

drongos are described by Vaurie (1948). The following species and regions are involved:

Edge of the African Rain Forest

D. adsimilis. Where the savanna races *adsimilis* and *divaricatus* come into contact with the forest race *coracinus,* the intermediate race *atactus* has developed.

Edge of Wet and Dry Zone in Ceylon

The earlier invaders of Ceylon were the wet zone subspecies *D. caerulescens leucopygialis* and *D. paradiseus lophorinus.* With the drying out of southern India a second wave of forms reached Ceylon in the dry country forms *D. caerulescens insularis* and *D. paradiseus ceylonicus.* Hybrid populations of the two species are found along the edge of the wet zone where *D. caerulescens leucopygialis* and *insularis* and *D. paradiseus lophorinus* and *ceylonicus* meet. This process of hybridizing has apparently been accelerated in recent years by the deforestation of Ceylon.

Two other areas in which there is some evidence for hybridization between divergent populations are the western side of the Gulf of Siam (*D. leucophaeus* and *D. macrocercus*) and central Annam (*D. paradiseus, D. leucophaeus, D. remifer*) (Vaurie, 1948).

In northern India, as well as in Burma, where the ranges of *Dicrurus paradiseus paradiseus* and *D. p. grandis* meet, an intermediate population (*"rangoonensis"*) is encountered. Since this population appears not to be more variable than the two adjacent ones of *paradiseus* and *grandis,* and since it extends (at least in Burma) over a considerable area, it seems hardly appropriate to consider it an area of secondary intergradation (hybrid population).

In the Yangtse Valley, where *D. leucophaeus leucogenis* and *D. l. salangensis* meet, some intermediate specimens are found. Not enough material is available to indicate whether the pale northern and the dark southern forms intergrade gradually or hybridize along an abrupt zone of contact.

All the described cases of hybridization among drongos can be classified as "allopatric" hybridization. This means that hybrid populations have developed in the zone of contact of two otherwise allopatric subspecies. However, there is a remote possibility that one island species owes its origin to (introgressive) hybridization. The above mentioned *D. andamanensis,* in addition to its *paradiseus*-like characters, has a crest much like *D. hottentottus.* Unless this is due to accidental parallelism, it appears possible that the *paradiseus*-like ancestor of *andamanensis* was modified by the infiltration of crest-genes from *hottentottus.* The reverse possibility seems less likely since *andamanensis* has the earmarks of an old endemic while *hottentottus,* as is indicated by the history of the species, must have reached the Asiatic continent only rather recently.

Clandestine hybridization. It is taken for granted in continental species that there is a considerable amount of gene exchange between neighboring populations and subspecies. On the other hand, as far as island subspecies are concerned, it is usually assumed that they are very efficiently isolated against each other. Study of a widespread island species, such as *D. hottentottus,* throws considerable doubt on this assumption. As Vaurie (1948) has shown, the thirty-two subspecies of this species are arranged in chains of related forms. Each link is more or less intermediate between neighboring links.

One of these chains is: *samarensis* (Samar)—*striatus* (Mindanao)—*morotensis* (Morotai)—*atrocaeruleus* (Halmahera)—*carbonarius* (New Guinea)—*laemostictus* (New Britain). Though each link on this chain owes its origin to colonization by the preceding link, it appears doubtful whether this alone can account for the clinal progressions along this chain. Nor can much of it be due to the environment which is very uniform in this tropical belt. It is more likely that a continuous exchange of individuals between neighboring island populations is responsible for at least part of these progressions. The degree of dispersal within each of the species is therefore one of the important evolutionary factors to be considered.

Dispersal

Birds can be classified, from the dispersal point of view, into species that cross water gaps freely and those that do not. Both kinds are found among the

TABLE 11. *Dispersal facilities of drongos*

A. Not found breeding on any island (4 species)
   1. *D. ludwigii* (Africa)
   2. *D. atripennis* (Africa)
   3. *D. annectans* (India)
   4. *Ch. papuensis* (considering New Guinea as being zoogeographically a continent)

B. On islands of the continental shelf only (3 species)
   1. *D. caerulescens* (Ceylon)
   2. *D. aeneus* (Formosa)
   3. *D. remifer* (Sumatra, Java)

C. On islands of the continental shelf and a few islands a little beyond the edge of the shelf (2 species groups)
   1. *D. leucophaeus* (islands west of Sumatra: Simalur, Siberut, Sipora, North and South Pagi; also Lombok)
   2. *D. paradiseus* (islands west of Sumatra: Simalur, Nias, Lasia, and Babi; also Andaman Islands, separated from the shelf by a gap of about 30 km. width); with *D. andamanensis* (Andamans, an earlier offshoot of *D. paradiseus*)

D. Freely colonizing oceanic islands (2 species groups)
   1. Superspecies *D. adsimilis* (Mascarene Islands)
   2. Superspecies *D. hottentottus* with *D. balicassius*

drongos. On the basis of their transoceanic dispersal, the drongos fall into four groups (table 11).

There are only two superspecies that are capable of freely colonizing oceanic islands: *D. adsimilis* and *D. hottentottus*. Neither of these two superspecies differs in its physical equipment (length and shape of wing, etc.) visibly from any of the other drongos. It is therefore probable that the dispersal faculties of these two superspecies are due to some difference either in their ecology or in their psychology. Perhaps they are more social than other drongos or less "afraid" of water areas? Whatever the factors be, the superspecies *D. adsimilis* has colonized Principe Island and most of the principal islands of the Mascarenes (Madagascar, Comoros, Mayotte, Aldabras).

Dicrurus hottentottus has an even more extensive range, and an analysis of its geographical variation (Vaurie, 1948) has shown that it has colonized oceanic islands on a large scale. Assuming arbitrarily that the species had its center of origin in the Philippines (any other assumption would yield similar results), the species made the following jumps across oceanic gaps: Luzon (*balicassius*)—Samar (*hottentottus samarensis*), Philippines—N. Moluccas, N. Moluccas—Celebes, N. Moluccas — Seran — Buru — Timor — Tenimber—Kei, Timor—Sumba—Lesser Sundas—Sumatra, North Moluccas—New Guinea—New Britain—New Ireland, New Guinea—Guadalcanal—San Cristobal, Buru—Celebes—Greater Sunda Islands, Palawan—Semirara—Tablas (fig. 5). *Dicrurus hottentottus* has thus jumped oceanic gaps a minimum of twenty times. This shows that, like *adsimilis*, it is a good transoceanic colonist. However, its jumps are relatively short, compared to those of *Zosterops*, *Myzomela*, *Aplonis*, and other Pacific birds, and *D. hottentottus* can get a foothold only on fair-sized islands with a varied rain forest. The species thus offers an ideal background for rapid speciation and this is exactly what it shows.

SUMMARY

(1) The family Dicruridae (drongos) consists of 20 Old World species, most of them tropical. Their classification is discussed.

(2) The evolution of the taxonomic characters of the family is investigated. The characters of the more specialized species, such as large size, frontal crests, long tails, and modifications of the outermost tail-feathers have arisen independently in different branches of the family. Evolution within the family has been restricted to a realization of a limited number of trends.

(3) Every species character varies geographically. This is shown for general size, pigmentation, proportions, and special structures (crests, tail-rackets).

(4) The geographical variation of many characters is not haphazard, but correlated with such features of the environment as temperature and humidity. Island birds are frequently larger or smaller than the

populations on the adjacent mainlands.

(5) The number of subspecies per species varies from 1 to 32, averaging 5. Some of these subspecies are very young since they have formed on new islands on the recently emerged Sunda Shelf.

(6) The most distinct subspecies, including all borderline cases between subspecies and species, are found along the periphery of the species range or at other very isolated locations.

(7) Double invasions of the same parental stock have led either to the existence of two sympatric species, as are *D. montanus* and *D. hottentottus leucops* on Celebes, and on the Andamans *D. andamanensis* and *D. paradiseus otiosus,* or to the formation of hybrid flocks (*D. caerulescens* and *D. paradiseus* on Ceylon).

(8) Two species groups, *adsimilis* and *hottentottus,* freely colonize oceanic islands. The other species, though not differing in their physical equipment, are limited to continental shelves and a few nearby islands.

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GEOGRAPHIC VARIATION AND SPECIATION IN APPALACHIAN SALAMANDERS (*Plethodon jordani* Group) *

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INTRODUCTION

The family Plethodontidae is the largest, the most flourishing, and the most highly specialized group of recent salamanders. Its early evolution seems to have taken place in the Appalachian Highlands, where a considerable percentage of the known species still live. The first plethodontids were undoubtedly mountain stream inhabitants. From this restricted habitat adaptive radiation headed each of three evolutionary lines toward terrestrialism. Two of these lines remained at least partially bound to water and are restricted to eastern North America. The third and truly successful group developed independence of water even for breeding and was then able to invade Europe and South America. Some forms have gone so far as to have become arboreal (species of *Oedipus* and *Aneides*) and to bear living young (*Hydromantes*).

Dunn (1926) and Piatt (1935), who have discussed in detail the lines of evolution summarized above, show that species of the genus *Plethodon* were probably the first to adapt themselves to environmental conditions that require no aquatic stage. It is with a group of closely allied forms of *Plethodon* that we are concerned here. By studying their type of speciation we hope to shed some light on the mode of salamander evolution in general. It should be remarked that our forms occur in the original home of the family. Their names follow in chronological order of description: *jordani, shermani, metcalfi, clemsonae, rabunensis,* and *melaventris*. Figure 1 shows the general topography of the area inhabited by these forms and Figure 11 their ranges.

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HISTORY

The knowledge of these salamanders [1] began in the summer of 1900 when Mr. L. E. Daniels, while collecting molluscs in the Great Smoky Mountains, dropped two salamanders in a bottle of alcohol. A year later these were named *Plethodon jordani* by Blatchley. Since then, a new form has been brought to light every eight years or so and the distribution of each has been delimited, chiefly by Dunn (1926), Bailey (1937), Bishop (1943), and Grobman (1944).

There is now general agreement in regard to the ranges of *jordani* and *shermani*, forms restricted to the Great Smoky and the Nantahala Mountains, respec-

* Contribution of Northwestern University and Chicago Natural History Museum.

[1] Variously known as the "*jordani*," the "*metcalfi*," and the "*jordani-metcalfi*" group.

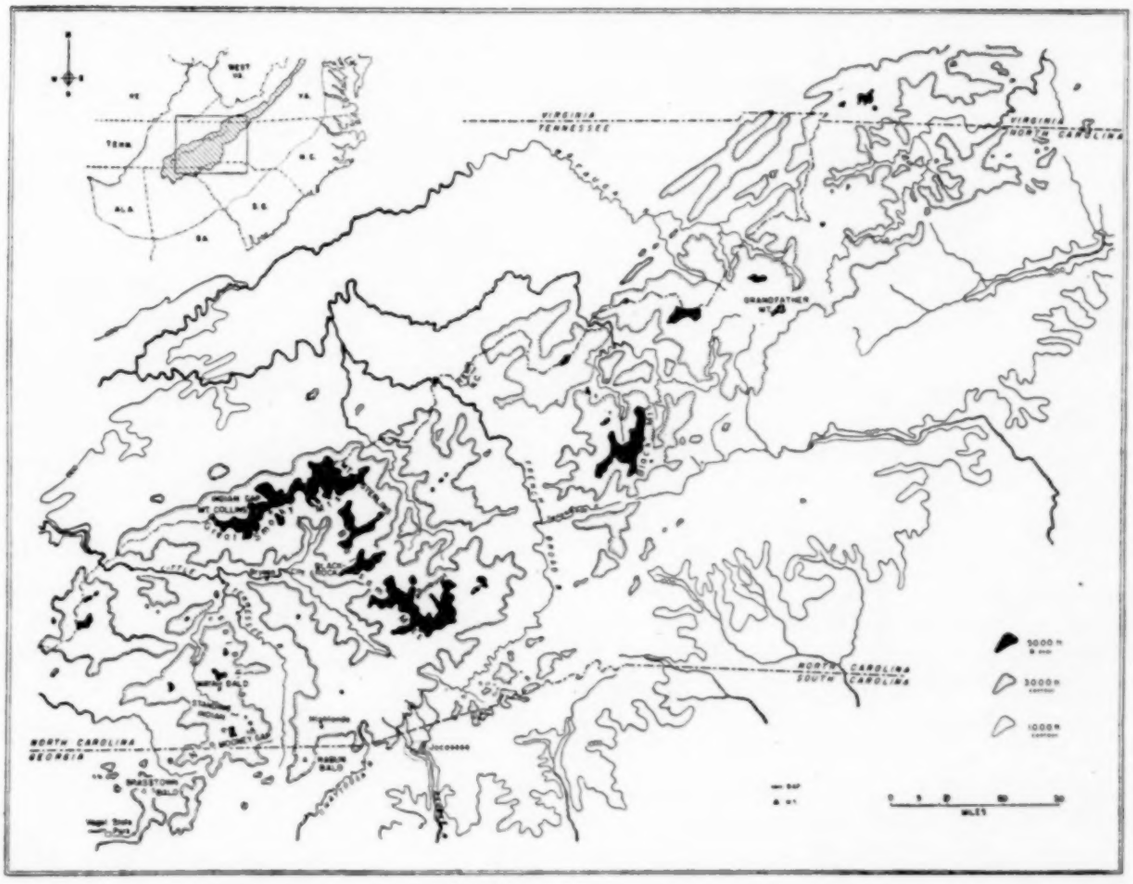

FIG. 1. Contour map of the southern Appalachian Highlands showing the places referred to in the text and the principal ranges and valleys. Corresponding area is outlined on inset map indicating Blue Ridge province (shaded) and limits of Appalachian Highlands (dotted line). Type localities are also included, as follows: SUNBURST: *P. metcalfi;* INDIAN GAP and MT. COLLINS: *P. jordani;* WAYAH BALD: *P. s. shermani;* JOCASSEE: *P. s. clemsonae;* RABUN BALD: *P. s. rabunensis;* HIGHLANDS: *P. s. melaventris;* 1.5 miles northeast of LINVILLE: *P. yonahlossee.* Map adapted from U. S. Coast and Geodetic Survey Sectional Aeronautical Charts R-8 and S-8 (Charlotte and Winston-Salem), 1936. (Linville lies southwest of Grandfather Mtn.)

tively. Two names (*rabunensis* and *melaventris*) have but recently been assigned by us, the former to the population of Rabun Bald, Georgia, the latter to the southern segment of a population long designated as *"metcalfi." P. clemsonae* has nearly always been applied to salamanders from Jocassee, a locality in extreme northwestern South Carolina. However, in 1944 Grobman used this name so that it included *"clemsonae"* of other workers with the blackbellied, southern segment of their *"metcalfi."* He thus disregards the dorsal and lateral markings of *clemsonae* but advisedly calls attention to the difference between the southern and northern populations of *"metcalfi."* Bailey had noticed this difference but associated it with altitude rather than with latitude.

ANALYSIS OF CHARACTERS

Our field observations and a study of ample fresh material collected by us indicate that only the analysis of the geographical distribution of the various characters, especially those of color, fully reveals the biological situation. We are therefore considering these in detail before taking up the taxonomically recognizable populations.

The definitive color characters in the

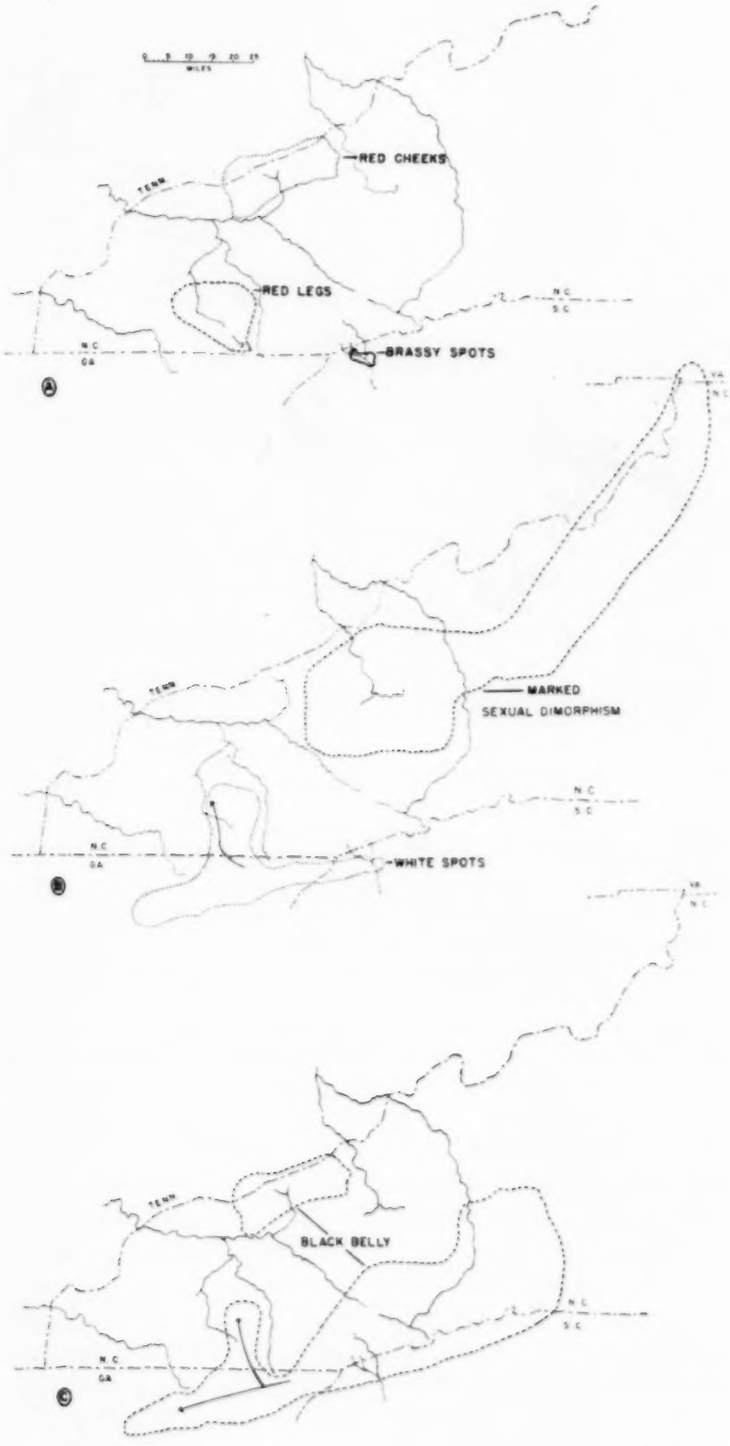

FIG. 2. Distribution of six characters among the populations of the *jordani* group. Arrows indicate *decreasing* incidence of characters. A. Distribution of red cheeks, red legs and brassy dorsal markings. B. Distribution of lateral white spots and marked sexual dimorphism. C. Distribution of black belly.

jordani group are: (1) red markings on the cheeks or legs; (2) white spots on the sides; (3) brassy flecks on the dorsal surface; (4) black ground color of the belly. Other characters are size and sexual dimorphism.

Color:

1. Red markings. Wood (1947, a and b) has indicated the close similarity of the juveniles of the two red-marked populations. All specimens less than 29 mm. in total length have red spots on the dorsum but lack red marks in the areas where they occur in adults.

Cheeks: Specimens having red cheeks are confined to the Great Smoky Mountains, from Mt. Sterling to the mountains north of Bryson City, North Carolina (fig. 2, A). With the exception of the *metcalfi* collections (see sexual dimorphism below), nearly all of the specimens from this area have red cheeks: 34 of 37, 76 of 78, and all but two of "several hundred" (Dunn, 1926; Pope, 1928; King, 1939; respectively).

Legs: Red-legged salamanders are confined to the Nantahala Mountains (fig. 2, A).[2] To the published records as summarized by Grobman [3] we add: Standing Indian Mountain, directly south of Wayah Bald and just north of the Georgia line; Mooney Gap,[4] east of Standing Indian and midway betwen it and the Little Tennessee River. The 23 specimens from Standing Indian show the same amount of red as a series of 18 topotypes from Wayah Bald. Although some individuals of the two series have the red reduced, all possess the character. The Mooney Gap specimens, on the other hand, show a marked reduction in the amount of red on the legs, and one of the twenty-four lacks the red entirely.

2. White spots. Populations having white spots (fig. 2, B) along the sides of the head and body are found along the southwestern periphery of the range of the *jordani* group, i.e., from Wayah Bald, North Carolina, to Jocassee, South Carolina, as indicated by the map. The maximum incidence of these white spots is found in the populations from Mooney Gap (21 of 24 specimens) and Rabun Bald (85 of 101 specimens). At Jocassee, to the east, the incidence is practically undiminished (14 of 17 specimens). Northwestward from Mooney Gap there is a significant decrease: 14 of 23 specimens at Standing Indian and 7 of 18 at Wayah Bald are white-spotted. Bailey's 31 specimens from Weatherman Bald and Tusquitee Bald lack white spots. These two mountains are about twelve miles west of Wayah Bald. There is thus a distinct cline from the southeastern to the northwestern Nantahala Mountains. All the remaining populations of this species group lack the lateral white spots.[5]

On the basis of the white spots and other characters, Bishop (1941) regards the red-legged population as closely (subspecifically) related to *P. glutinosus*. Grobman (1944) wisely rejects this relationship, and we present the following additional evidence.

An examination of living *Plethodons* under the highest feasible magnification (about 50 ×) shows that the white spots are divisible into two distinct types. One of these types is found in *P. yonahlossee* and *P. glutinosus* (both from the Black Mountains, Buncombe County, North Carolina). The pseudopodia of the white pigment cells (guanophores) tend to overlie the dermal glands and invade the ad-

[2] A single specimen with red spots on the legs was recorded by Dunn (1926) from Mt. Sterling in the Great Smoky Mountains.

[3] Grobman's easternmost record is apparently Franklin. Since this town is in a flat valley we conclude that the specimen actually came from the Nantahala Mountains to the west.

[4] Mooney Gap is on the southern flank of Bearpen Mountain at 4500 feet altitude. The series herein designated as from "Mooney Gap" actually includes three individuals from nearby Reynolds Gap (3700 feet) on the northeastern flank of Picken's Nose, which is adjacent to Bearpen Mountain.

[5] Breder and Breder (1923) record a single white-spotted individual from Ashe County, North Carolina, at the opposite extremity of the group range.

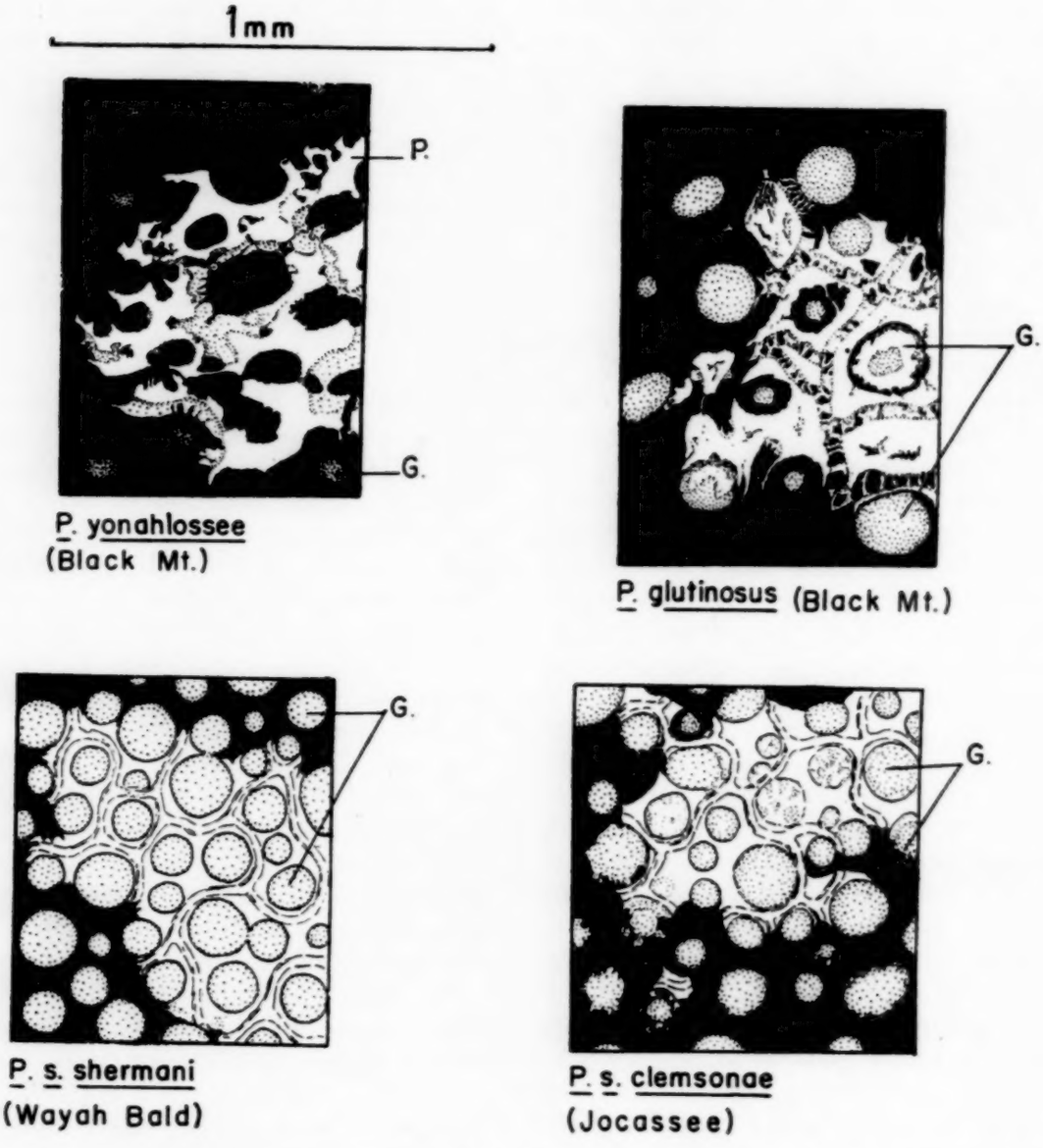

FIG. 3. Lateral white spots in *Plethodon* magnified about 50 times; G. for gland, P. for pseudopodia. Note the numerous pseudopodia formed by the guanophores of *P. yonahlossee* and *P. glutinosus* and their complete absence in *P. s. shermani* and *P. s. clemsonae*. All drawings from living specimens. *P. yonahlossee* and *P. glutinosus* from the Black Mountains, Buncombe County, North Carolina; *P. s. shermani* and *P. s. clemsonae*, topotypes.

jacent black area, as shown in figure 3. The other type of white spot was found in salamanders from Wayah Bald and Jocassee, obviously distinguishable from *glutinosus* by the presence of red legs or brassy markings. Due to the absence of the underlying black pigment and the failure of the guanophores to produce evident pseudopodia, these white spots appear as sharply delimited areas (fig. 3), though actually less conspicuous than the other type of spot.

3. Brassy markings. All of our eleven specimens from Jocassee (fig. 2, A) have conspicuous brassy specks crowded together on the dorsum. In some, these markings cover the back; in others, they are reduced to more or less discrete areas. Bishop's two specimens also had these markings but Brimley described the dorsal

markings of the type series variously as "white," "greyish" and "frosted with white." We assume that these terms apply to the markings that we call "brassy." Only this low-altitude population restricted to Jocassee exhibits this character.

4. Black belly. The black (or dark) belly is the only character with a discontinuous distribution (fig. 2, C). It is found in the Great Smoky Mountains and over a large area in the southern part of the group range. (The specimens we rate as "light" or "pale" are not entirely devoid of melanin.)

Only occasional individuals from the Nantahala Mountains have black bellies, except for the Mooney Gap series from the extreme southeast, where 7 of 24 are so colored. This series is clearly intermediate between the other Nantahala populations and the ones from Rabun Bald, where virtually all adults have black bellies.

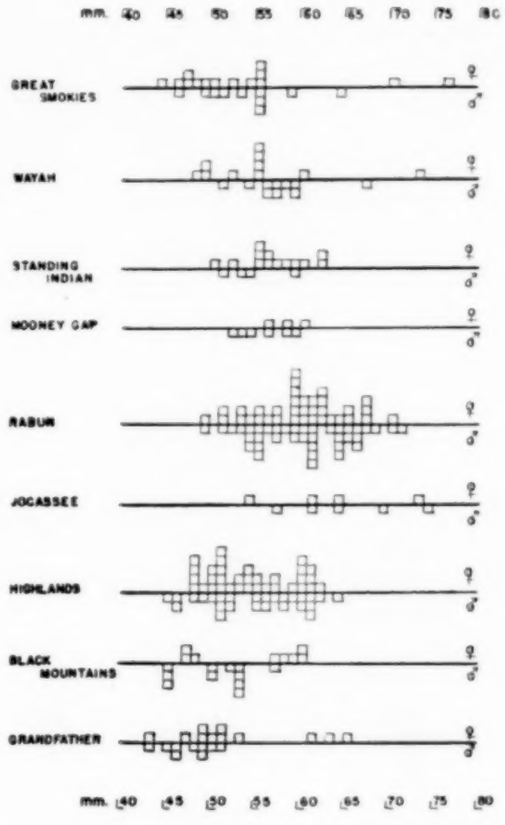

FIG. 4. Size distribution in nine populations of the *jordani* group.

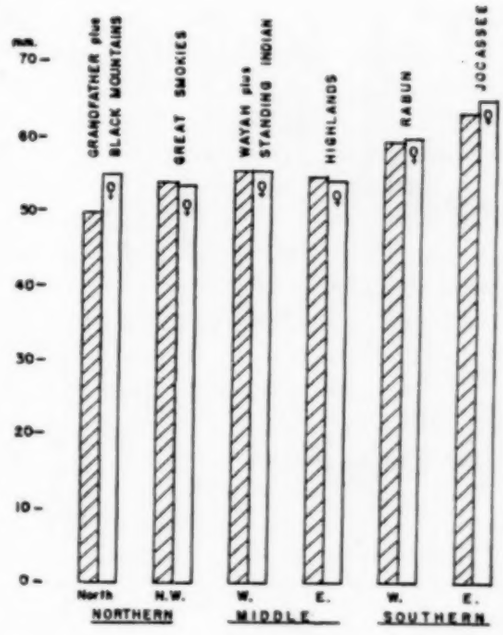

FIG. 5. Average size of the sexes of the *jordani* group, beginning at the left with the northern populations. The size gradient is more pronounced in the males than in the females.

This quantitative character is a troublesome one because its analysis calls for direct comparison of uniformly preserved material. We agree with Grobman that belly-color is darker in the southern populations; unlike him, we have no difficulty in allocating specimens from the Highlands-Brevard area to the dark-bellied population. It should be mentioned that only adults can be used in analyzing this character, because juveniles of all populations have pale bellies.

Size and sexual dimorphism:

Considerable variation in length is evident between the populations of the *jordani* group. The longest specimens come from the south (Jocassee and Rabun Bald), the shortest from the north (Grandfather Mountain). The remaining populations are made up of individuals intermediate in length (fig. 4). Thus there is more or less decrease in body size from south to north (fig. 5). This tendency is strengthened by altitude as well as by latitude, since the southernmost popu-

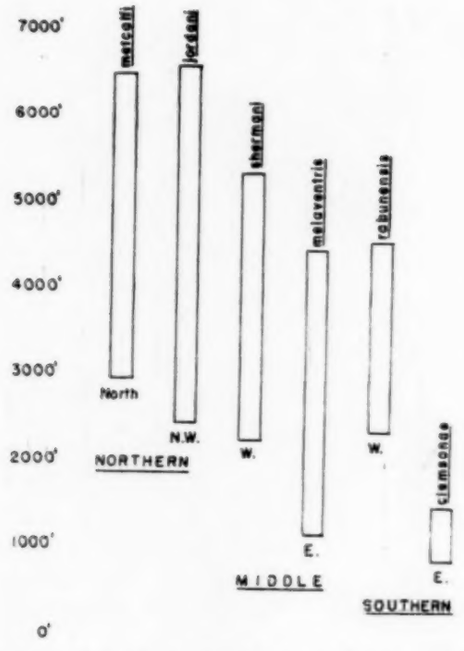

FIG. 6. Vertical distribution of the members of the *jordani* group, beginning at the left with the northern forms.

lations are also found at the lowest elevations (fig. 6).

Due to a marked dimorphism in the northeastern populations (Grandfather Mountain and the Black Mountains), the differences between samples of the populations in mean length are more pronounced if the males are compared separately. Bailey's series from Blackrock in the Balsam Mountains exhibited a similar difference between the sexes. The distribution of populations with this marked sexual dimorphism is shown on the map (fig. 2, B).

In addition to this, the bilateral swelling of the snout of the males is most pronounced in this northeastern population. This seems to be correlated with the degree of development of the mental gland.

Vomerine teeth:

The number of vomerine teeth possessed by the members of the different populations (fig. 7) approximately parallels general size as in other genera of the Plethodontidae. Specimens from Jocassee and Rabun Bald have the longest vomerine series, those from Grandfather Mountain have the shortest.

SYNTHESIS OF CHARACTERS

Besides the incidence of occurrence, the degree of development of the characters is also instructive in comparing populations. Although 96 per cent of the specimens from Mooney Gap had some red on the legs, nearly all had reduced amounts

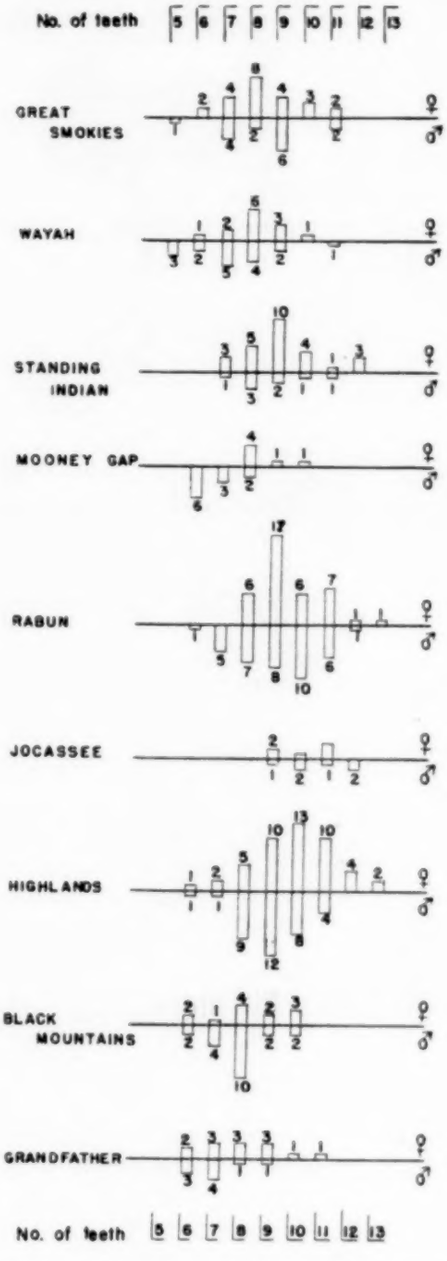

FIG. 7. Number of vomerine teeth in nine populations of the *jordani* group.

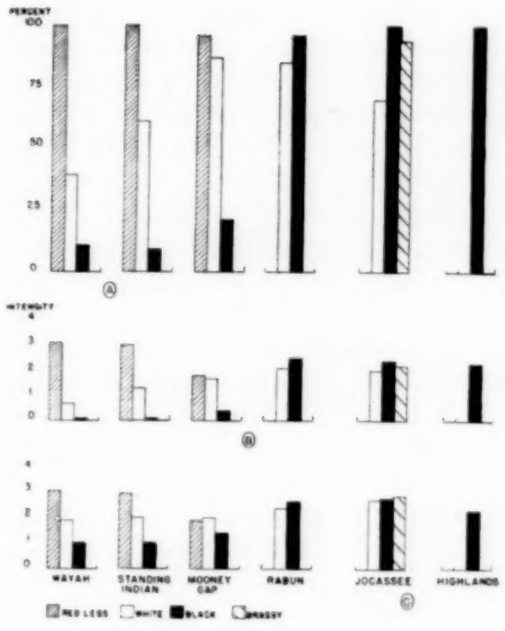

FIG. 8. Variation in six populations of *Plethodon shermani* as indicated by four color characters: red legs; lateral white spots; black belly; brassy dorsal markings. Histograms separated by spaces proportional to distance between localities. A. Incidence of occurrence. B. Average intensity based on all specimens (maximum 4, minimum 0). C. Average intensity based only on specimens possessing the characters (maximum 4, minimum 1).

as compared with the Wayah Bald and Standing Indian populations. We have represented this type of phenomenon graphically for four color characters in figure 8, B and C. In constructing these charts, an arbitrary scale was set up; the preserved specimens were separated into four groups according to the development of the character, with the lowest number standing for the weakest development.

There are two ways of representing the amount of development of a character in a population: In figure 8, B, we have averaged the intensity for all specimens collected in a locality; in figure 8, C, only the intensity of those that possess the character, since it may be maintained that negative ones should not be included. The pictures presented are the same. Preferring the former procedure, we have put the histogram of figure 8, B on the map (fig. 9).

The populations of salamanders in the northern areas are sharply separated by all characters analyzed. In contrast to this, each of the southern populations possesses at least one character in common with all neighboring ones. It would

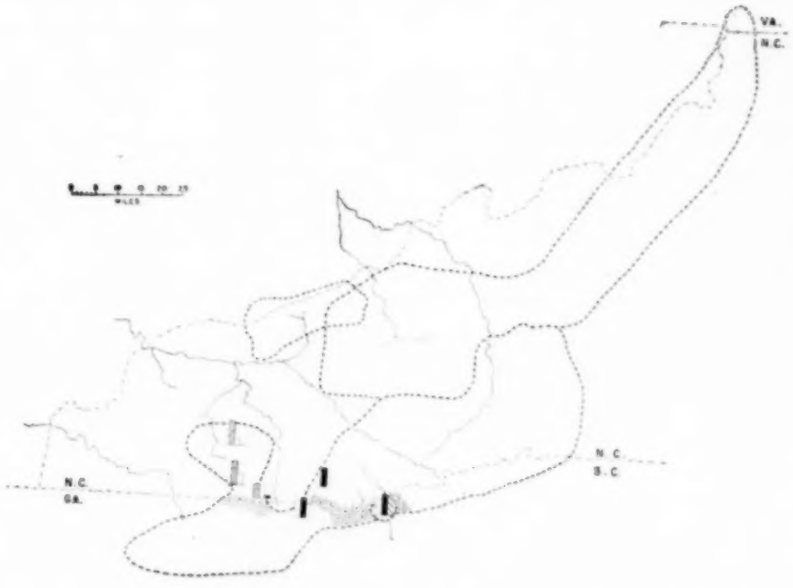

FIG. 9. Distribution of specifically distinct members of the *jordani* group (broken lines) and of the populations analyzed by the histograms of figure 8, B. Probable areas of intergradation indicated by dotting.

thus appear that gene flow has ceased between the salamanders from three areas, one extensive southern area and two northern ones (fig. 9). The two northern forms overlap geographically and vertically (King, 1939) with no evidence of intergradation, a situation that requires further study. Within the large southern area, outlined on the map, there is continuing gene flow, as evidenced by the overlapping distribution of four color characters.

Taxonomy

Considering the *jordani* group as a whole from the taxonomic standpoint, the two northern forms are properly designated as species distinct from each other and from the southern forms. The northwestern one continues to be known as *Plethodon jordani;* it is confined to the Great Smoky Mountains and has red cheeks. As shown by Grobman (1944), the name *Plethodon metcalfi* must be restricted to the northeastern form, which exhibits marked sexual dimorphism and is light bellied. Its specific distinctness from the southern form rests upon the lack of intergradation of these two characters despite the absence of an evident physiographic barrier.

As regards the southern populations, the characters analyzed in the foregoing section overlap in such a way that any taxonomic arrangement must be somewhat arbitrary. The chief difficulty lies in the distribution of white spots: Were it not for this character, there would simply be a narrow zone of intergradation between salamanders with red legs and those with black bellies. The white spots, however, reach their maximum incidence in this narrow zone around the headwaters of the Little Tennessee River. They disappear gradually to the northwest, and abruptly to the northeast (fig. 8). In considering nomenclature, it is no more proper to ignore this character than any other.

The oldest name applicable to any of these southern forms is *Plethodon shermani,* assigned by Stejneger (1906) to red-legged specimens from the Nantahala Mountains. We regard the remaining members of this southern complex as subspecies of *shermani.* The black-bellied, low-altitude population from Jocassee, most examples of which have brassy dorsal markings and white lateral spots, are designated *P. s. clemsonae* Brimley. We have recently (1948) assigned two names to the remaining southern salamanders. These are *P. s. rabunensis* from Rabun Bald, a population with black bellies and white lateral spots, and *P. s. melaventris,* the unmarked population found to the north and east of the other subspecies of *P. shermani.* Both of these have long been known as *metcalfi.*

Dunn lists *metcalfi* from Brasstown Bald, Georgia; Long Island, Alabama; between Andrews and Aquone, North Carolina. These are the three southernmost records, and actually lie beyond the range of *P. shermani.* It is interesting to note that Howell (1909) lists *P. shermani* from Brasstown Bald. Bailey however, relegates all of the Alabama and Georgia specimens to *P. glutinosus* except those from Rabun Bald, Georgia. The specimen from between Andrews and Aquone is apparently *shermani,* as Bailey and Grobman conclude. In view of the similarity of *P. s. rabunensis* to *P. glutinosus* we have examined all of the available specimens from northern Georgia. Two of these (USNM 86834–5) cannot be assigned to *glutinosus.* These two specimens from Vogel State Park, Lumpkin County, Georgia, although hard and shrunken, are definitely assignable to *P. s. rabunensis.* One has white lateral markings of the *shermani* type; the other is unmarked. The vomerine tooth counts, 10–9 and 9–8, are low for *glutinosus,* and the bellies of both, "1" on our scale, are paler than any *glutinosus,* all of which we would rate as "3" or "4." Howell's single specimen (USNM 45358) from Brasstown Bald is apparently *rabunensis* (vomerine teeth 9–8, belly "3"). It is in a worse state of preservation than the Vo-

gel specimens. Bailey's large series from Vogel State Park and adjacent Blood Mountain (UMMZ 76334–66) are definitely *glutinosus,* having black bellies, high tooth-counts, and extensive white spotting of the *glutinosus* type.

The following key will be helpful in identifying the six forms of the *jordani* group:

Red markings
  Cheeks red (Great Smoky Mountains). *P. jordani*
  Legs red (Nantahala Mountains). *P. s. shermani*
No red markings
  With other markings
    Brassy dorsal markings and white lateral spots (Jocassee) ..... *P. s. clemsonae*
    White lateral spots only (northeastern Georgia) ..... *P. s. rabunensis*
  Immaculate
    Belly black (South of Balsam Mts. and Swannanoa R.) ..... *P. s. melaventris*
    Belly pale (North and east of *melaventris*). *P. metcalfi*

Considerable difficulty may be encountered in separating *P. s. melaventris* from *P. metcalfi.* In this case, the provenance of the puzzling specimens should be helpful.

Evolution and Intrageneric Relationships

Primitive characters in the genus *Plethodon* are large size, long vomerine series, lack of sexual dimorphism, and a colored dorsal pattern (either spots or a stripe). Considering these characters collectively, *metcalfi* is the most specialized member of the group, and *clemsonae* is the most primitive. Of the remaining four, *rabunensis* is next to *clemsonae,* whereas *shermani, jordani* and *melaventris* cannot be arranged in sequence with certainty. *P. s. shermani* and *jordani* are primitive in the retention of dorsal markings in the juveniles, but *melaventris* has longer vomerine series. *P. jordani* is smaller than the other two, although the difference is slight and may not be significant. However, since it is a distinct species, and more like *metcalfi* in altitudinal distribution, it may be ranked next to that form in degree of specialization.

In altitudinal distribution *clemsonae* is sharply set off from the other forms as the only one confined to and occurring in the low elevation on the edge of the Piedmont plateau. The other five ascend to the tops of the humid, forested mountains on which they live and, with the exception of *melaventris,* descend to elevations between 3000 and 2300 feet. *P. s. melaventris* occurs as low as 1200 feet. We conclude that the tolerance for low altitude in *clemsonae* is further evidence of its primitiveness. This form appears to be a relict, confronted on the south by the drier and mostly deforested Piedmont country, and on the north by its close relative, the more successful *melaventris* (fig. 10). The locality inhabited by *clem-*

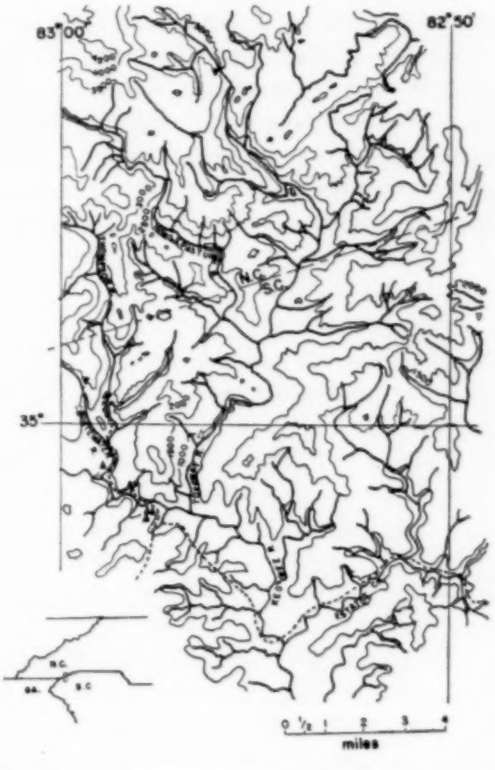

Fig. 10. Contour map of the headwaters of the Keowee River, showing collecting sites of *Plethodon shermani clemsonae* (triangles) and *P. s. melaventris* (inverted triangles). Contour interval 500 ft. Adapted from U. S. Geological Survey, Pisgah and Pickens Quadrangles. Inset map shows location of area.

sonae also harbors the relict plant *Shortia galacifolia,* which has a closely similar if not identical range (House, 1907).

There is a trend for the more specialized members of the *jordani* group to be increasingly restricted to higher elevations with increasing latitude. This is contrary to expectations, which would place the more southern forms at higher altitudes.

The key to the situation seems to lie in the relationships of this group to the other large species of *Plethodon* inhabiting the area, namely, *glutinosus* and *yonahlossee.* Superficially, resemblance of the *jordani* group, especially *rabunensis,* is more to *glutinosus* than to *yonahlossee,* but this may be due to parallel evolution. The group is closer to *glutinosus* in the smaller number of vomerine teeth, but is more like *yonahlossee* in retention of the dorsal color pattern and general body proportions. As far as tooth-counts are concerned, the loss of vomerine teeth occurs independently in many plethodont genera, and *P. wehrlei,* admittedly close to *yonahlossee,* has few vomerine teeth.

Of some importance are the geographical and ecological relations. *P. glutinosus,* although partially separated altitudinally from certain members of the *jordani* group, overlaps all of them geographically. *P. yonahlossee,* on the other hand, is separated geographically from all of the *jordani* group except *metcalfi,* the most specialized member (fig. 11).

Without raising the question of whether geographic variation is the universal method of speciation (Mayr, 1942, 1947), such variation evidently occurs within the *jordani* group. There is no reason to doubt that the original separation was achieved in this manner. The region has been ideally suited to this type of speciation since the close of the Paleozoic.

If the present distribution, geographical and vertical, is of any value in determining phylogenetic relationships, *yonahlossee* rather than *glutinosus* appears to be the ancestor of the *jordani* group, a conclusion not unwarranted on morphological grounds. This theory postulates:

(1) Speciation by geographic isolation into *yonahlossee* (northern) and the ancestor of the *jordani* group (southern).

(2) Speciation (evidently still geographic) of the *jordani* group.

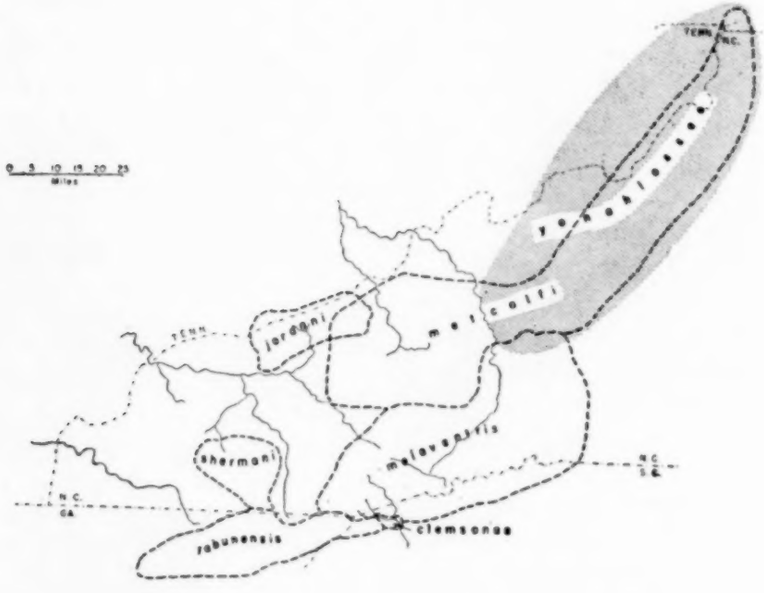

FIG. 11. Distribution of the members of the *jordani* group (broken lines) and of *P. yonahlossee* (shaded). *P. glutinosus* is widely distributed in the eastern United States.

(3) Invasion of the range of *yonahlossee* by *metcalfi*, the most specialized and presumably the most ecologically divergent, and consequently the least competitive, member of the *jordani* group.

It may be argued that *glutinosus* is the ancestor of the *jordani* group and that the present situation is the result of a re-invasion by *glutinosus*. The difficulty here lies in the fact that the overlap by *glutinosus* is most complete in the case of the primitive, low-altitude members of the *jordani* group and least complete in the case of the high-altitude *metcalfi*. This species would presumably be the most divergent ecologically, and would therefore offer the least amount of competitive resistance to such re-invasion.

The ecological argument for *yonahlossee* ancestry is based on the assumption that in the varying requirements of the *jordani* group, *metcalfi* is furthest from the original. We realize that theoretically the reverse may be true, but there is no supporting evidence. Morphological and ecological changes are generally correlated, especially in the Plethodontidae (cf. *Desmognathus*).

Although Bishop (1941) has stated that the group is derived from *glutinosus*, and others have implied the same, Bailey (1937) doubts that such is the case.

Divergence Within the Group

In considering speciation within the *jordani* group, rivers and mountain ranges are both a help and a hindrance, since it is not always clear which have been the isolating factors. Following the original separation from *yonahlossee* by the French Broad valley, the first isolation was that of *metcalfi* in the northeast. The evidence for this is the greater specialization of this form, as well as its present range on both sides of the French Broad River. We advance the thesis that the territory now occupied to the northeast of this river represents an extension of the original range. *P. metcalfi* has been able to extend its range because it occupied the favored northeastern position, this being the only direction in which any member of the group could find suitable ecological conditions. To the south, west and northwest, the mountains end abruptly, limiting the remaining members of the *jordani* group about to their original positions.

Following the separation of *metcalfi*, the second step was the isolation of *jordani;* this is borne out by its obviously close alliance to *shermani*, as seen especially in the juveniles of the two forms. The isolation of *jordani* from *shermani* apparently was accomplished by the deepening of the valley of the Little Tennessee River (Bailey, 1937). It is interesting to note that *metcalfi* has been able to invade the eastern end of the range of *jordani*, although there must be considerable competition between the two species.

The remaining members are still connected, although tenuously so, especially around the headwaters of the Little Tennessee River. It is likely that the area east of the French Broad and south of the Swannanoa Rivers, now occupied by *melaventris*, represents an extension of the range of this form, as the area is largely lacking in territory suitable to *metcalfi* with its preference for high altitudes.

Summary

Geographic variation in the *Plethodon jordani* group was studied by analyzing a number of characters in large samples from nine critical localities. Three allopatric forms between which gene flow has apparently ceased were distinguished on the basis of this analysis; one of these is polytypic, the other two monotypic.

The characters analyzed overlap in such a way in the polytypic form that the situation cannot be accurately represented by nomenclature. This necessitates a somewhat arbitrary taxonomic assignment of names to the various populations.

Speculations are made on phylogeny and relationships. These speculations are based on the morphology and on the present distribution, not only of the *jordani* group but of certain more primitive spe-

cies of *Plethodon* as well. The conclusion is that speciation has resulted from geographic isolation, a process that is evidently continuing.

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